

VOLUME VI

UNIVERSITY OF HAWAII

NUMBER 4

NOV 17 1941

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# MADROÑO

A WEST AMERICAN JOURNAL OF  
BOTANY



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Published at North Queen Street and McGovern Avenue, Lancaster,  
Pennsylvania

October, 1941

# MADROÑO

## A WEST AMERICAN JOURNAL OF BOTANY

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Entered as second-class matter October 1, 1935, at the post office at Lancaster, Pa., under the act of March 3, 1879.

Established 1916. Published quarterly. Subscription Price \$2.50 per year. Volume I, Numbers 1 to 17, complete, \$5.00. Volume II, Numbers 1 to 17, complete, \$5.00. Volume III, Numbers 1 to 8, complete, \$5.00. Single numbers \$0.75.

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## FURTHER STUDIES ON MONOTROPOIDEAE

HERBERT F. COPELAND

This paper continues a series (5, 6, 7, 8, 9), of which the account of *Sarcodes* by Doyel and Goss (12) is to be considered a unit. It records observations on *Pterospora*, *Hypopitys*, and *Monotropa*, and adds to the previous account of *Hemitomes* (*Newberrya*).

It has been a pleasure to acknowledge from time to time the unstinted cooperation of various institutions and individual correspondents. The following have facilitated the preparation of the present contribution: the Herbarium of the University of California; the Dudley Herbarium of Stanford University; the Herbarium of the California Academy of Sciences; Dr. W. L. Jepson; Mr. Willman Spawn; Dr. W. H. Camp; Dr. P. L. Zimmerman; and the Oregon Biological Supply Company.

## PTEROSPORA ANDROMEDEA Nuttall

*Pterospora andromedea* was described by Nuttall (25) as collected "In Upper Canada, near the Falls of Niagara. Mr. C. Whitlow." There has been essentially no nomenclatorial confusion as to this plant; no segregation of species or varieties has been proposed; Small (28) cites a single obscure synonym. The plant is common in the mountain ranges of western North America; rare eastward to the region of the type locality.

The material studied was collected from time to time at Jonesville, Butte County, California, at an altitude of about five thousand feet. There the plant shares the habitat of *Sarcodes* and *Pleuricospora*, in forests of fir (*Abies concolor*). As compared with its congeners, *Pterospora* emerges from the ground and flowers noticeably later in the season; it is usually in full anthesis late in July.

The shoots come up from globular masses of roots. It is noticeable that whereas they emerge in the neighborhood of dead shoots of the previous year, they are not in immediate contact with such dead shoots, nor at a distance to be measured in centimeters, but a meter or more away. Jepson (19) believes that the plant is monocarpic, and it is probable that he is correct. There is, however, the possibility that the scattered shoots come up from long roots which have emerged from the masses. This is suggested by the behavior of the generality of monotropoid plants, in which the genetic individuals are polycarpic, forming shoots year after year as adventitious buds on the same root system. A positive determination of this matter could be attained only by determining the course of individual roots in a mass of humus, and I have not undertaken it.

The standard accounts of the gross structure of the shoot, as by Jepson and Small, leave essentially nothing to add. The tall and slender stems, densely glandular, are of a light purplish red color. The greater part of each shoot is a rather lax bracted raceme, usually but not always exhibiting orthodox phyllotaxy. The recurved glandular pedicels bear no bractlets. The five glandular sepals are separate. The five petals form a glabrous sympetalous urceolate corolla, yellowish in color, becoming chartaceous in age. Each of the ten stamens bears two horns on the back of the anther. The globular ovary is belted at the base by a nectary from which ten evenly spaced lobes project between the bases of the filaments. Internally, the ovary is five-chambered below, one-chambered above, filled by massive placentae bearing numerous ovules. The stigma is obscurely five-lobed, the lobes opposite the petals, that is, at the ends of the carpels.

MacDougal has described the anatomy of the vegetative parts. The stem includes a cylinder of bundles so closely packed as almost to be continuous; around this there is a well developed continuous sheath of fibers.

The vascular supply of the flower (pl. 8, fig. 1) enters the receptacle as a cylinder. From this there depart radially, first, five sepal bundles, and then, alternating with them, five petal bundles. There are no gaps above these bundles. Five stamen bundles arise as branches from the upper sides of the petal bundles. Above the departure of the petal bundles the stele breaks up into a ring of ten bundles. Of these, the five which are opposite the sepals bend outward and fork periclinally; the outer branches constitute the supply to the five remaining stamens; the inner ascend the ovary wall in the planes of the septa, and are to be interpreted as fused pairs of lateral bundles of adjacent carpels. The five remaining bundles enter the ovary in the planes of the locules, being the planes of the petals and carpels; each of them is a fused pair of ventral bundles of a single carpel. They branch out into the placentae and disappear. In several features the vascular system just described is peculiar. No other monotropoid plant is known to be without carpel dorsals (though they are not well differentiated from carpel laterals in *Sarcodes*); in none do the placental bundles lie in the planes of the petals. Here it is as though the proper placental bundles had swung outward into the ovary wall, and the carpel dorsals inward, into the placentae. In most plants of the group, the style is supplied by the carpel dorsals, which ascend in the thin bands of tissue between the ridges projecting into the style channel. *Sarcodes* is exceptional in that the placental bundles supply the style, ascending within the ridges. In *Pterospora*, lacking carpel dorsals and having the placentals in a peculiar position, the style is without vascular tissue.

As is known, the anther (pl. 8, figs. 2-7) projects horizontally toward the style from the summit of the filament, and bears two



horns, inserted respectively on the two sides of the insertion of the filament and projecting toward its base. A vascular bundle runs from the summit of the filament to the inward end of the anther; by this it is known that the inward end is distal, the end bearing the horns proximal, the upper side dorsal, and the lower side ventral. There are four parallel horizontal pollen sacs; the dorsal ones are larger than the ventral. A cross section shows the epidermal cells extended into conical points on the dorsal and ventral, but not the lateral, surfaces. Between the epidermis and the tapetum there are some two or three layers of wall cells; near the horns a few of these cells develop reticulate lignified thickenings, as in the endothecium of a typical flowering plant. A similar structure has been reported in *Sarcodes*, and will be reported below in *Monotropa*; it is less extensive in *Pterospora* than in these other genera, being apparently merely a relic structure. The cells of the tapetum become binucleate. The pollen grains are four-grooved.

Dehiscence of the anther begins by two vertical slits, each of which crosses the proximal ends of the two pollen sacs of one lobe of the anther. Formation of these slits amounts to the same thing as the dehiscence of the anthers of *Sarcodes* or *Monotropis*, being, as I take it, the typical dehiscence of the anthers of *Ericales*. Subsequently two secondary slits develop from the middles and at right angles to the primary ones, that is, in the plane between the two pollen sacs of each lobe of the anther. By a general shrivelling of the walls of the anther, accompanied by growth of the connective, these secondary slits gape widely; it is through them that most of the pollen escapes. Drude's (13) figure of the fully dehiscent anther is accurate, though it gives a false impression that the connective becomes torn in a horizontal plane from proximal to distal.

The internal surface of the ovary wall is covered by two layers of well developed fiber-like cells.

A complete series of stages of the development of the seed has not been seen, and there is nothing to add to my earlier notes (4). The embryogeny appears to be altogether typical of the group. The integument is of two layers of cells. The wing on the seed is of two layers of cells. It commences to form, by proliferation of the epidermis of the integument at the chalazal end, before the embryo sac is fully developed.

#### HYPOPITYS MONOTROPA Crantz

Only two species of monotropoid plants were known to Linnaeus (23). One, known in English as the pine-sap, occurs on all continents of the north temperate zone; the other, the Indian pipe, occurs in North America and eastern Asia, but not in western Asia and Europe. The oldest Latin designation of the pine-sap seems to be *Orobanchae quae hypopithis dici potest*, of Bauhin (1671). It is of course no *Orobanche*; Tournefort (1706)

gave it as name the adjective *Orobanchoides*; Dillenius (1719) took up the substantive designation recorded by Bauhin, as *Hypopitys*. The Indian pipe, first recorded by Plukenet (1671) under *Orobanche*, was named *Monotropa* by Gronovius (about 1740). Linnaeus included both species in one genus, for which he used the name *Monotropa*, the species becoming respectively *M. Hypopithys* and *M. uniflora*. The breach of priority as to the generic name was immediately protested by Hill (16): "Linnaeus takes away its received name *hypopitys* and calls it *monotropa*." Because he was the first after 1753 to use *Hypopitys* as the name of a genus, Hill is cited as authority for it; this in spite of the facts, that he did not originate it, and that he did not use binomials and cannot be cited as authority for any of the species. Binomials under *Hypopitys*<sup>1</sup> were first made by Crantz (10), the pine-sap becoming *H. Monotropa* and the Indian pipe *H. uniflora*.

Inasmuch as the first post-Linnaean authors gave to *Hypopitys* exactly the extent which Linnaeus had given to *Monotropa*, it might be held that the two names are exact synonyms, and that *Hypopitys* is not available as the name of any genus. On the other hand, the pre-Linnaean history shows that the two names are based on different types, and that if the pine-sap is placed in a different genus from the Indian pipe its name is *Hypopitys*. Such in effect was the conclusion of the pre-type-system authors Nuttall (25) and Bentham and Hooker (1); such was the conclusion of Small (27), who made the combination *Hypopithys Hypopithys*. Repeating binomials being excluded by our rules, we must accept the first specific epithet published after 1753; this yields, as has been shown, the combination *Hypopitys Monotropa*. We might be glad to reject this combination as a matter of taste; it has gone almost completely unaccepted since its original publication; but the rules are designed to spare us the responsibility for a choice.

I follow Kamienski (21) and Domin (11; this work has been a most valuable guide to the history and literature) in recognizing only one species of *Hypopitys*. There are considerable variations, and Small (28) has recognized five species in North America alone; but these variations seem so inconstant as to make the recognition even of varieties a critical matter.

The available material preserved in liquid has included several roots, stems, and flowers collected by Dr. W. H. Camp, in Oregon, Ohio, and Tennessee, and two shoots with nearly ripe fruit collected by Mr. Willman Spawn in Rock Creek Park, Washington, D. C., in July of 1938.

<sup>1</sup> Variations in the spelling will be noted. I have not consulted the pre-Linnaean publications. Linnaeus wrote *Hypopithys*, Hill and Crantz *Hypopitys*. These are mere variant spellings; but we are forbidden by rule to meddle with them. In using the word as a specific epithet, we must follow Linnaeus; in using it as a generic name, we must follow Hill.



Nothing is here added to knowledge of the gross structure. The shoots originate endogenously in roots, a mass of which constitutes the permanent organ of the plant. Domin, after a long discussion of the literature, concludes that the underground structures are not true roots, but an axis not differentiated as root or stem, to be called the *Prokaulom* (anglicizable as *procaulon*). I have not examined these structures, but the conclusion is inescapable, from Kamienski's (20, 21) description and from what is known of the other monotropoid plants, that Domin is mistaken. As Christoph (3) has shown, the occasional more or less complete suppression of some of the characters of roots—the cap and endogenous branching—depends on the presence of mycorrhiza. The same effacement of character appears in the roots of other plants when they are beset with mycorrhiza.

The shoot is usually yellowish and more or less pubescent. The upper part of it constitutes a bracted raceme. When it emerges from the ground, the raceme is bent to one side, and the buds or flowers are crowded and more or less pendant; later the axis and pedicels become erect and the flowers or fruits become separated. At its maximum the shoot is rarely twenty-five centimeters tall.

The lateral flowers (pl. 8, fig. 8) stand in the axils of bracts whose margins vary from entire to lacerate. There are no bractlets; four sepals, a lower pair placed laterally and an upper pair placed dorsally and ventrally with regard to the flower; four separate petals with saccate bases, alternating with the sepals; eight stamens; a nectary with eight horn-like lobes arranged in pairs which clasp the bases of the petalad stamens; a pistil, the ovary four-chambered below, one-chambered above, the stigma obscurely lobed, the lobes opposite the petals. Variations in the proportions of ovary and style, as well as in color, pubescence, and the indentation of the margins of the bracts, have been utilized for subdivision of the species.

Older accounts definitely described the terminal flower as pentamerous. I have not found such a flower. I believe that in the few shoots preserved in liquid which I have examined the terminal flower has been suppressed. The highest flower has been tetramerous, the pedicel embraced by two bracts instead of one (evidently as a result of shortening of the last internode, the one above the insertion of the flower), the lower pair of sepals somewhat removed from the flower.

Domin cites many authors who have disagreed as to whether the outer envelope of the flower is really a calyx, and its segments sepals: Eichler is the chief authority in the affirmative, Baillon in the negative. He quotes observations of Irmisch (17) and Wydler (30) and gives his own, to the effect (a) that the upper pair of leaves of this envelope are, one or both of them, often suppressed; (b) that the lower pair are often somewhat withdrawn from the base of the flower; (c) that these leaves, espe-

cially the lower pair, often have buds in their axils. He concludes that they are not true sepals, but elevated bractlets in process of conversion into sepals. It seems to me unreasonable to recognize a calyx in course of coming into existence in any group as advanced as Ericales: rather, any irregularities are to be interpreted as matters of degeneration. Since *Allotropa* is the only positively asepalous genus of the monotropoid group; since only *Monotropis* and sometimes *Allotropa* have definite bractlets; we may interpret the facts assembled by Domin in some such fashion as this: the structures of *Hypopitys* now under consideration are positively sepals; they are affected by a tendency to degeneration; it is possible that a tendency to produce bractlets, almost completely extinct in this genus, retains enough strength to affect the course of the degeneration.

Kamienksi has accounted in full for the anatomy of the vegetative parts; I have here only to describe the vascular supply to the flower. One bundle from the circle in the stem turns outward. It becomes flattened tangentially and presently splits into three branches, of which the middle one supplies the bract while the two on the sides swing together and unite as a cylinder ascending the pedicel. All this is quite the same as in the genera previously studied. The cylinder of vascular tissue ascending the pedicel becomes compressed in the dorso-ventral plane, so as to approximate a four-sided prism (pl. 9, fig. 10). From each of its faces there departs a sepal trace, leaving a small gap or none. The traces to the lateral sepals depart at a much lower level than those to the dorsal and ventral sepals; this is in harmony with Domin's observations as to the relative positions of the sepals. The petal bundles emerge as broad bands from the angles of the prism; each promptly forks into three, of which the one in the middle is the smallest and descends under the sac of the petal, while the larger lateral ones ascend past the sac. The petalad stamen bundles are not fused with the petal bundles, but are closely associated with them; each originates as a pair of bundles at the sides of a petal bundle, the pair drawing together and uniting above the petal bundle. The sepalad stamen bundles emerge at the edges of the siphonostele as it breaks up. The carpel dorsals, well developed in the ovary walls and style, are only with difficulty traced to their origin; the feebly developed provascular strands that lead into them seem to originate typically as paired strands beside, above, and resembling the petalad stamen bundles. Foster (15) has recently quoted Gregoire to the effect that floral

#### EXPLANATION OF THE FIGURES. PLATE 8.

PLATE 8. *PTEROSPORA ANDROMEDEA*. FIG. 1. Model of the vascular system in the receptacle  $\times 50$ . *Ca*, sepal bundles; *Co*, petal bundles; *St*, stamen bundles; *Cl*, carpel laterals; *Pl*, placental bundles. FIGS. 2, 3. Juvenile stamens,  $\times 10$ . FIG. 4. Longitudinal section of juvenile stamen,  $\times 50$ . FIG. 5. Cross section of juvenile stamen at the plane marked *x* in fig. 4,  $\times 50$ . FIG. 6. Area marked *x* in fig. 5,  $\times 400$ . FIG. 7. Cross section of dehiscent stamen,  $\times 50$ . *HYPOPITYS MONOTROPA*. FIG. 8. Old flower in which the fruit is nearly ripe,  $\times 5$ .



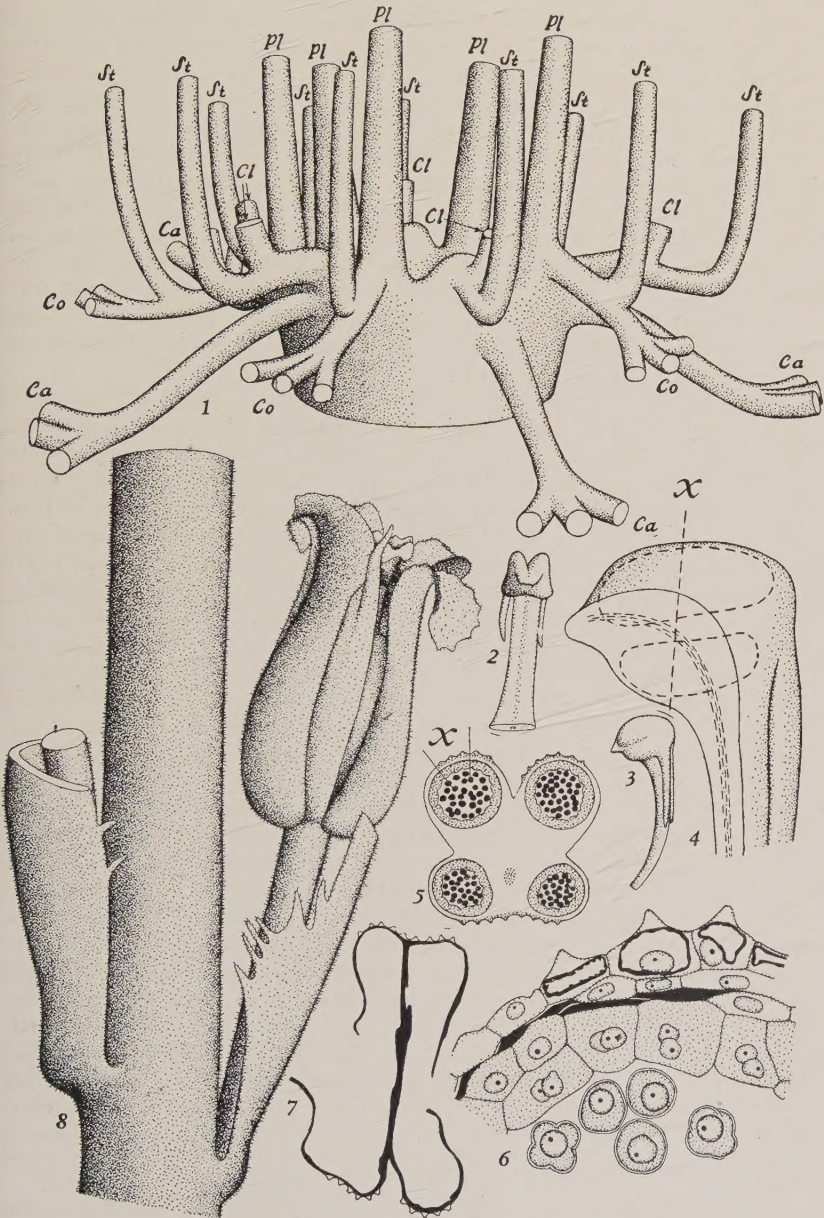


PLATE 8. PTEROSPORA ANDROMEDEA; HYPOPITYS MONOTROPA

leaves are distinguished from vegetative leaves by acropetal development of the vascular supply. The carpel dorsals of *Hypopitys* (and likewise, as will be seen, of *Monotropa* and *Hemitomes*) constitute an exception to this principle. The breaking up of the siphonostele finally yields one bundle to each lateral placenta, and two each to the dorsal and ventral placentae. This seems to be an outcome of the bilateral character of the whole vascular system. It is as though the ventral bundles of adjacent carpels were fused at the sides of the flower, but not at the front and back.

It is regretted that no anatomical study has been made of young stamens. The anther opens by two vertical slits at the outer, presumably proximal, end; these slits meet above, separating a small outer valve from a large inner one; and soon the valves liberate the pollen by swinging widely apart. Young stages and old ones (pl. 9, figs. 11, 12) respectively agree exactly with corresponding stages of *Pityopus* as illustrated by Eastwood (14). It is particularly regretted that the position of the pollen sacs was not ascertained; though it may be presumed that there are four in each anther, lying horizontally, each slit of the anther crossing the ends of two of them. The pollen grains are two-grooved.

The fruit is a capsule, its inner surface covered by a single layer of elongate cells not distinguished by staining reactions.

The development of the seed has been described in detail by Koch (22). I have seen only one stage, conforming well to Koch's account, and so beautifully clear that I could not refrain from drawing it (pl. 9, fig. 9).

#### MONOTROPA UNIFLORA L.

Of the name of this genus and species enough has been said above. The genus is apparently monotypic; no variation even of varietal rank is recognized as occurring within the United States. *Monotropa coccinea* Zuccarini, of Mexico and Central America, and *M. australis* Andres, of Colombia, were treated as varieties by Domin.

The available material preserved in liquid has included six collections, as follows: (1) Three shoots purchased some years ago from the New York Biological Supply Company, as a museum specimen, without collection data. (2) Three shoots presented by the Oregon Biological Supply Company; collected by R. E. Griffin, Bullrun, Oregon, July 11, 1939. The fluid preserves the white color of the plants, and makes specimens excellent for museum use rather than for sectioning. (3) A number of shoots presented by the Herbarium of the University of California, without collection data. (4) One shoot, with roots, furnished by Mr. Willman Spawn; collected in Rock Creek Park, Washington, D. C., July, 1938. (5) One shoot, with roots, furnished by Dr. P. W. Zimmerman; collected in the arboretum of the Boyce Thompson Institute for Plant Research, New York, summer, 1939.



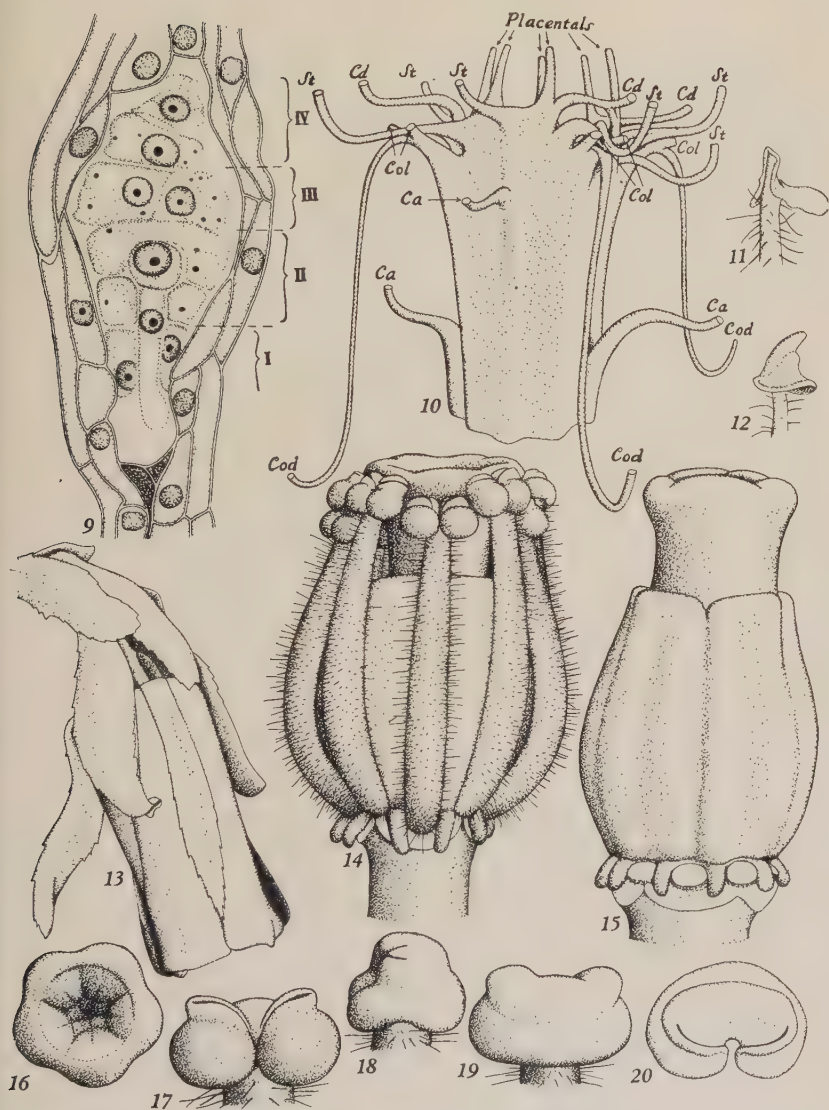


PLATE 9. *HYPOPITYS MONOTROPA*. FIG. 9. Longitudinal section of nearly ripe seed  $\times 400$ . The endosperm, at a certain early stage, is four-celled; the Roman numerals I-IV indicate the derivatives of these cells. FIG. 10. Model of the vascular system in the receptacle  $\times 12.5$ : *Ca*, sepal bundles; *Cod*, petal dorsals; *Col*, petal laterals; *St*, stamen bundles; *Cd*, carpel dorsals. FIGS. 11, 12. Dehiscence anthers  $\times 10$ . *MONOTROPA UNIFLORA*. FIG. 13. Flower  $\times 2.5$ . FIG. 14. Flower with perianth removed  $\times 5$ . FIG. 15. Pistil  $\times 5$ . FIG. 16. Stigma  $\times 5$ . FIGS. 17-20. Anthers  $\times 10$ .

(6) Roots, shoots, flowers and fruits furnished by Dr. W. H. Camp; collected in central New York State at various times.

As is well known, the erect shoots are in life white, like paraffin (the austral races mentioned above are distinguished by red color); dried, or placed in most preservatives, they turn black. The stem is clad with spiral scales; study of a single example showed the spiral to be orthodox. The solitary flower (pl. 9, fig. 13) is terminal on the recurved summit of the stem. Domin has quoted many conflicting authorities as to whether or not sepals are present. I find that a varying number of scales may project past the base of the flower. Of these, sometimes none and sometimes one is inserted so immediately below the petals that it can be regarded as a sepal. It is not particularly different from the leaves, and I have not found more than one. The five separate petals overlap at the margins so as to form a campanulate corolla about fifteen millimeters long. Each petal is saccate at the base and truncate at the apex, sometimes with an apiculation. There are ten stamens, manifestly in two whorls, the lower opposite the petals. The densely pubescent filaments are curved inward and bear the subglobular anthers pressed against the lower side of the stigma (pl. 9, fig. 14). The ovary is belted at the base by a ten-lobed nectary; the lobes are cylindrical; they are obscurely but perceptibly paired, clasping the bases of the petalad stamens. The ovary is ovoid, marked by five deep longitudinal grooves opposite the petals, that is, in the median planes of the carpels; and by five shallow grooves between them where the carpels meet (pl. 9, fig. 15). A shallow circular depression at the summit of the ovary is filled by the base of the short, stout, obconical style. The stigma is five-lobed, the lobes opposite the petals and surrounding an unusually large crater-like depression which leads into the style passage. The depression is lined by five masses of tissue which stand above the grooves, not the ridges, in the style passage. The surfaces of the five masses of tissue are more or less wrinkled, and the grooves in the style passage are obscurely continued upward upon them to some distance (pl. 9, fig. 16).

The stem resembles in its anatomy that of *Pterospora* rather than those of *Monotropis* and *Hypopitys*. It shows in cross section a ring of separate strands of xylem and phloem (in most specimens seriously shattered by shrinkage, apparently during fixation, a difficulty commonly encountered also in *Sarcodes* and *Pterospora*). Around the cylinder of bundles there is a continuous sheath of pericyclic cells with thinly lignified walls, being imperfectly developed fibers.

At the summit of the stem the sheath disappears. Exactly ten bundles enter the receptacle (pl. 10, fig. 25). Each of the five lying in the planes of the petals breaks up, typically, into five. Of these, the middle one is the petal bundle; it forks further into three, a small petal dorsal which follows the contour of the sac, and two larger petal laterals which ascend past it. The behavior



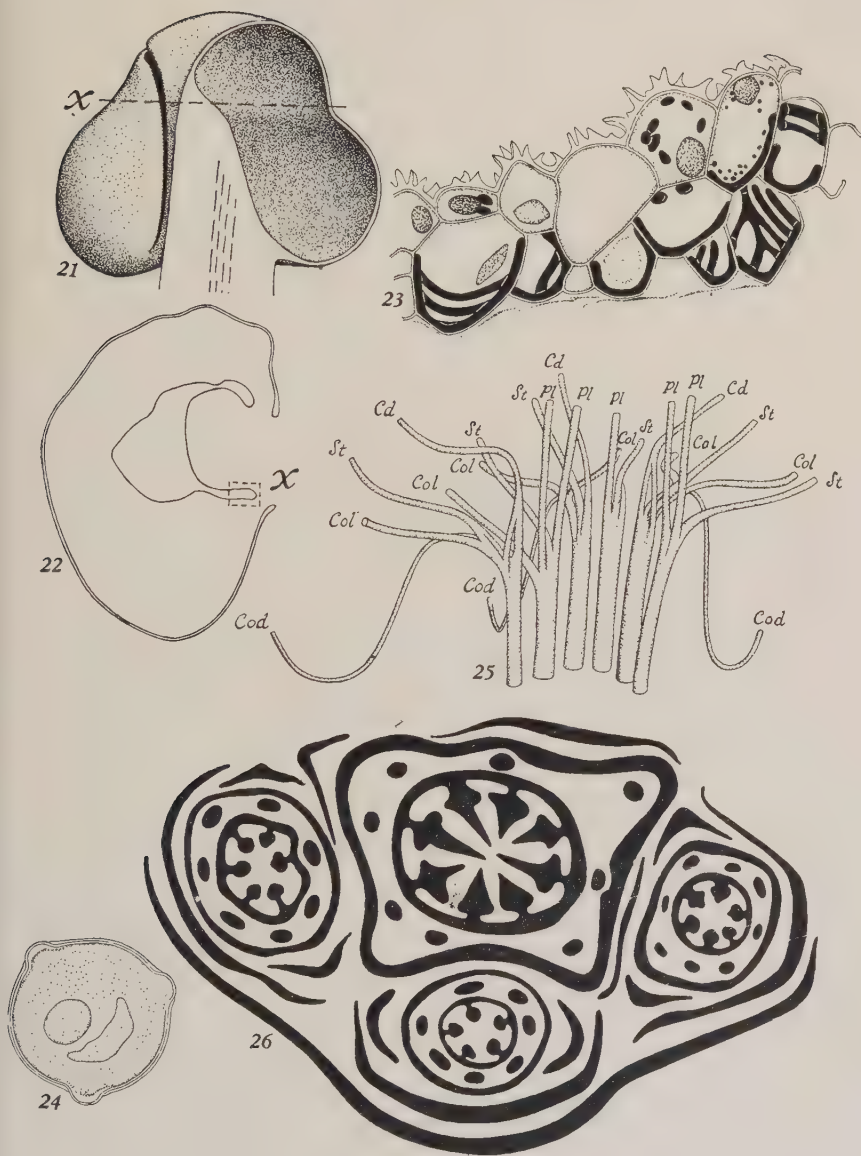


PLATE 10. *MONOTROPA UNIFLORA*. FIG. 21. Longitudinal section of anther  $\times 25$ . FIG. 22. Cross section of anther at the plane indicated by *x* in fig. 21  $\times 25$ . FIG. 23. Area marked *X* in fig. 22  $\times 400$ . FIG. 24. Pollen grain  $\times 900$ . FIG. 25. Model of half of the vascular system in the receptacle  $\times 12.5$ : *Cod*, petal dorsals; *Col*, petal laterals; *St*, stamen bundles; *Cd*, carpel dorsals; *Pl*, placental bundles. *HEMITOMES CONGESTUM*. FIG. 26. Cross section of primary flower with three secondary flowers in the axils of the sepals  $\times 10$ .

of these petal bundles is quite the same as in *Monotropsis*, *Hypopitys*, and *Pityopus*. The two bundles adjacent to the petal bundle unite above it to form a petalad stamen bundle, and the two marginal branches unite to form a carpel dorsal which is traced with difficulty here at its origin. As to the five bundles which enter the receptacle between the planes of the petals, each of these forks into three: the middle one supplies a stamen of the upper whorl; the lateral ones enter the placentae, being ventral bundles of adjacent carpels. The figure shows minor deviations from the assumed typical structure as just described: one of the petal lateral bundles does not originate from a proper petal bundle; one of the placental bundles is suppressed. The carpel dorsals enter the style and ascend it for some distance, but they are there poorly developed.

If the anther (pl. 9, figs. 17-20; pl. 10, figs. 21-23) is correctly understood, the outer end is proximal, the inner distal, the upper side dorsal and the lower ventral. At anthesis it includes a single chamber. Apparently (these points were regrettably not established) there are in the juvenile anther four horizontal pollen sacs, of which the ventral pair are much the larger. Dehiscence is through two curving slits at the proximal end; in dried material, and doubtless in life, these slits flare open as gaping pores. Along the margins of the slits the anther walls, elsewhere of one layer of collapsed cells, are of two layers, the walls of the inner layer bearing reticulate lignified thickenings as in a normal endothecium (pl. 10, fig. 23). Jepson states that the slits eventually meet, so as to convert the anther wall into two valves. This is not true in such fruiting material as I have seen; on the contrary, the pores retain their individuality until the plant dies and decays. The pollen grains (pl. 10, fig. 24) are three-grooved. The tube nucleus stains poorly and becomes distorted; the generative nucleus remains globular and deeply staining, and is surrounded by a clear space (not shown in the figure), the generative cell.

The inner surface of the ovary wall is covered by a single layer of somewhat elongate cells not distinguished by staining reactions.

Of the stages in the development of seed, we know only the structure of the mature ovule. It was described and figured long since by Campbell (2) quite as in *Hypopitys*.<sup>2</sup>

<sup>2</sup> Since the above was written Dr. Zimmerman has had the kindness to send a beautiful collection of fruiting material made in the Arboretum of the Boyce Thompson Institute in late summer of 1940. The seeds are much as in *Allo-tropa*; they are elongate, having a tail at each end; the embryo, borne on a suspensor, is usually of two cells; the endosperm has a haustorium at each end. It is now known that haustoria are produced on the endosperm in *Sarcodes*, *Allotropa*, *Monotropa*, and probably (to reinterpret a former observation) in *Monotropsis*; and that they are not produced in *Hypopitys* and *Pleuricospora*. I suppose that the absence of haustoria in these two genera is a result of parallel evolution and that the classification given at the end of this paper, in which *Hypopitys* falls near *Monotropa* and *Monotropsis* and far from *Pleuricospora*, may stand.



## HEMITOMES CONGESTUM Gray

Under the name of *Newberrya*, I have given a partial description of this rather uncommon plant of the Pacific Coast of North America, and have quoted from Jepson; but Jepson's description and mine require extension and amendment.

The original generic name *Hemitomes* was rejected by Torrey (29) as inappropriate; and the rejection was maintained by Small (28) on account of the priority of *Hemitomus* L'Her. Torrey's objection is of no standing in modern nomenclature; and Small's is disposed of by the rule (26) "When the difference between two generic names lies in the termination, these names must be regarded as distinct, even though differing by one letter only." Small recognized five species. Jepson has reduced three of these, whose type localities are in California, to synonymy with the type species. With this I fully agree, and I add the one which Jepson omitted as outside his area. I am glad to remark that Professor John Davidson has tended to support this action, in a paper read at Seattle in June, 1936; and that Dr. W. H. Camp has done so in private correspondence. The synonymy, then, is as follows:

*Hemitomes congestum* A. Gray, *Pacif. Rail. Rep.* 6: 80. 1857. *Newberrya congesta* Torr. in Gray, *Bot. Calif.* 1: 464. 1876. *N. spicata* A. Gray, *Proc. Am. Acad.* 15: 44. 1879. *Hemitomes pumilum* Greene, *Erythea* 2: 121. 1894. *Newberrya subterranea* Eastw., *Proc. Calif. Acad. Sci.*, ser. 3, 1: 80. 1897. *Hemitomes spicatum* Heller, *Cat. No. Amer. Pl.* 5. 1898. *H. subterraneum* Heller, *op. cit.* *Newberrya longiloba* Small, *No. Amer. Fl.* 29: 18. 1914. *N. pumila* Small, *op. cit.*

The Herbarium of the University of California has a photograph of the type of *Newberrya spicata*, and a photograph and a duplicate of *Suksdorf 2168*, the type of *N. longiloba*. I have been particularly helped by Dr. Jepson, who loaned a specimen collected by W. G. Wright, the type of *H. pumilum*. Two collections preserved in liquid have been available: (1) One shoot without roots, furnished by Dr. L. R. Abrams, who collected it in the California State Redwood Park, Santa Cruz County, June 14, 1934. (2) Several shoots and roots collected by Dr. W. H. Camp at Sol Duc Hot Springs, in the Olympic Peninsula, Washington, August 5, 1932.

Shoots, arising endogenously from roots, vary in height, the flowers being borne approximately at ground level; they expand in ascending, when well developed exceeding two centimeters in diameter at the base of the inflorescence. The inflorescence is essentially a bracted spike, often so brief and compact as to be accounted a head; in Abrams' specimen the phyllotaxy, both of the leaves below the inflorescence and of the flowers, is orthodox, the apparent divergence being  $3/8$  or  $5/13$ . Depauperate shoots may bear a single flower; on the other hand, vigorous shoots may bear axillary branches with one or more flowers, and may develop

secondary flowers in the axils of the sepals of the primary flowers. This behavior was noted on dissection of the type of *H. pumilum*; of Abrams' specimen; and of a specimen by C. A. Reed in the Herbarium of the California Academy of Sciences. Jepson's words, "Inflorescence . . . composed of short 2- to 5-flowered spikelets" imply that it is normal; but I find it only in a minority of the specimens; I do not find it in Camp's preserved material. The flowers (pl. 11, fig. 27) are practically always tetramerous; the four sepals are oriented as in *Hypopitys* and *Pleuricospora*, dorsally, ventrally, and laterally, the dorsal and ventral sepals being not infrequently suppressed. The sympetalous corolla is variable in length, from less than one centimeter to nearly two centimeters long. The four lobes alternate with the sepals, and are separate to a depth of more or less than one-third the total length of the corolla. The dried corolla is very fragile, and it is hard to be certain as to how deep the sinuses extend. *Newberrya longiloba* was distinguished by particularly deep sinuses, but I do not find these in our duplicate of the type. Indentation of the corolla lobes is variable; the retuse apex mentioned in my former account was merely the character of an individual. Stamens are normally eight, anthers dehiscing by two lengthwise slits on the outside; lobes of the nectary moderately prominent, evenly spaced; carpels eight, alternating with the perianth parts and stamens, so that the parietal placentae, and the lobes of the stigma, standing above them, are opposite the stamens and perianth parts.

Secondary flowers are usually in the axils of the lateral sepals, but may appear also in the axils of dorsal and ventral sepals (pl. 10, fig. 26). In the cluster figured, there is a second pair of scales, like sepals, above the lateral secondary flowers, as if the scales subtending these were bractlets: *Hemitomes* would have afforded Domin even better evidence than did *Hypopitys*, that the outer floral envelope is no true calyx. But what is the scale in whose axil is the dorsal secondary flower? And what is the scale on the ventral side of the primary flower, if not a sepal? I regard the scales subtending the lateral secondary flowers as sepals; and the scales above these flowers as a secondary pair of sepals, anomalously developed in connection with the anomaly of buds in the axils of the primary pair. The secondary flowers ordinarily have parts in smaller numbers than the primary ones, as two sepals, seven or six stamens, seven, six, or five carpels. They are later in development than the primary flowers.

The vascular system in the stem, as reconstructed from sections of Abrams' specimen (pl. 11, fig. 30), is a cylinder interrupted by very large leaf gaps; as there are no other gaps than these, and as the vascular tissue runs in broad oblique bands rather than in slender vertical bundles, it may be regarded as a siphonostele. The leaf traces, emerging at the bases of the gaps, fork into three as they enter the scales. Flower traces are not at all united with the traces to the subtending scales; the supply to



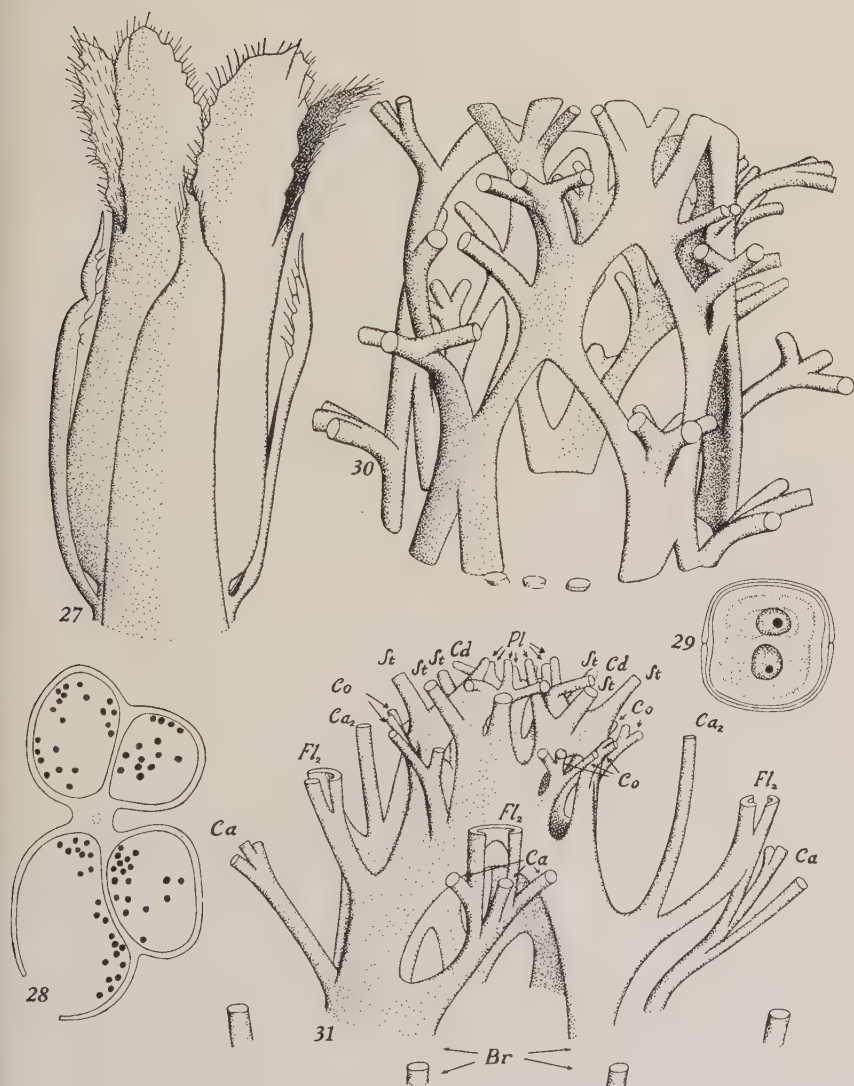


PLATE 11. *HEMITOMES CONGESTUM*. FIG. 27. Flower  $\times 5$ . FIG. 28. Cross section of juvenile stamen  $\times 50$ . FIG. 29. Pollen grain  $\times 900$ . FIG. 30. Model of the vascular system in the stem  $\times 5$ . FIG. 31. Model of the vascular system of the cluster of flowers shown in fig. 26  $\times 15$ ; *Br*, bundles to the bract; *Ca*, sepal bundles; *Fl<sub>2</sub>*, supplies to secondary flowers; *Ca<sub>2</sub>*, secondary sepal bundles; *Co*, petal bundles; *St*, stamen bundles; *Cd*, carpel dorsals; *Pl*, placental bundles.

each flower consists of two bundles springing from the sides of the gap above one of the upper leaves.

The figure of the vascular system of a primary flower with its attached secondary flowers (pl. 11, fig. 31) was constructed from a series of sections of Abrams' specimen, one of which yielded the diagram (pl. 10, fig. 26). The two bundles of the flower trace approach one another, become flattened, and unite as a siphonostele. Before this union is complete, four sepal traces emerge as single bundles above which there are large gaps. It seems that a secondary flower is typically supplied, like a primary flower, by two bundles springing from the sides of the gap left by the supply to the subtending leaf, which is in this case a sepal. Actually, we find that the secondary flower placed on the left in the figures is supplied as just described; the one on the right is partially so supplied, and partially from the sepal trace; the third, the dorsal secondary flower, is supplied entirely from the trace to the subtending sepal. The single bundles to the secondary sepals of the primary flower arise next to two of the secondary flower bundles. Each petal is supplied by two bundles which leave a single gap in the stele. Beyond these the stele emits three whorls each of eight bundles: stamen bundles, one opposite each perianth segment, all apparently in one whorl, not at all associated with the petal bundles; carpel dorsals, alternating with the stamen bundles, very poorly developed at the base, so that formerly I failed to discover their origin; and placental bundles, opposite the stamen bundles.

Juvenile stamens were found in the secondary flowers. The anther is borne vertically on the summit of the filament and includes four parallel vertical pollen sacs, of which the two on the dorsal side are much the larger. (I was formerly mistaken in making the ventral sacs the larger.) Dehiscence is through vertical slits on the dorsal sides of the dorsal sacs; the wall between the two pollen sacs of each lobe breaks down, and the whole outer wall swings around to the ventral side of the anther as a broad valve.

The cells of the inner surface of the ovary wall are not differentiated except perhaps by smaller size.

No new observations have been made upon the development of seeds; all that is known is that the ovules are essentially like those of *Hypopitys* and other members of the group.

#### DISCUSSION

In concluding the previous paper of this series, I put forward a tentative scheme of classification of the plants construed as constituting the subfamily Monotropoideae of family Ericaceae:

Tribe Pterosporeae: *Pterospora*, *Sarcodes*, *Allotropa*.

Tribe Monotropeae: *Monotropsis*, *Hypopitys*, *Pityopus*, *Monotropa*, *Monotropastrum*, *Wirtgenia*?

Tribe Pleuricosporeae: *Pleuricospora*, *Newberrya*, *Cheilotheca*?



Observations have now been extended to all of the above-named genera which are native in North America. Not a few of my previous statements have been found to require correction. A summary of the observations constitutes a formidably extensive table (Table 1). The data there assembled enable one to construct a tentative phylogenetic tree (text fig. 1) and to reconsider the proposed scheme of classification.

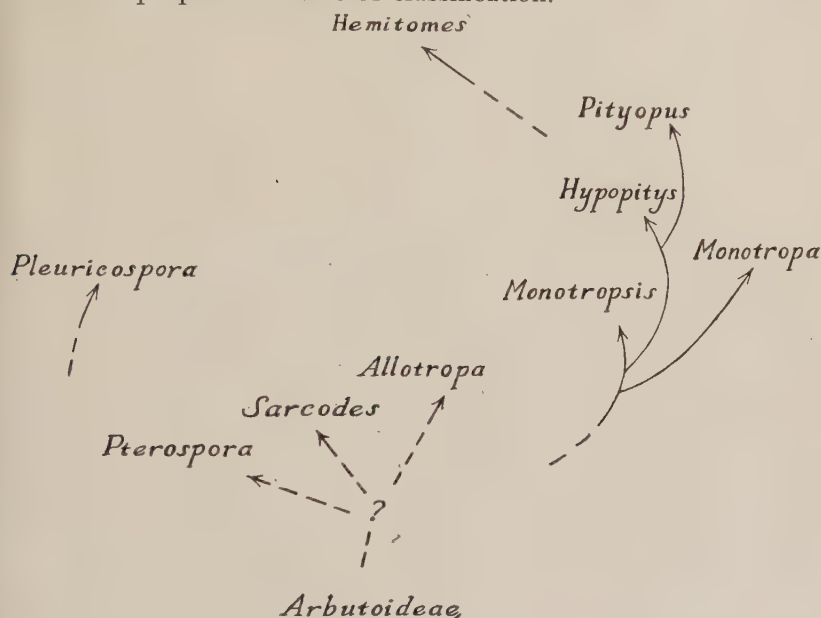


FIG. 1. Apparent phylogeny of the Monotropoideae.

*Pterospora*, *Sarcodes*, and *Allotropa* continue to appear more primitive than the other genera. The primitive features are tall and erect habit; bright coloration; axile placentation in the lower part of the ovary; evenly spaced lobes of the nectary; corolla sympetalous, urceolate (in *Pterospora* and *Sarcodes*); bractlets present (in some specimens of *Allotropa* only); anthers horned (in *Pterospora* only); anthers not permanently erect. The only single characters which separate these genera as a group from the others are the habit and the coloration; but the combination of characters, lobes of the nectary not paired and anthers not erect, is also distinctive. In all this, there is nothing to raise doubt as to the status of the tribe Pterosporeae as a natural group; often a primitive group can be distinguished from several derived groups taken together only by a combination of negative characters. Doubt appears when, on the other hand, we compare these genera with the supposed ancestral group Arbutoideae. The primitive characters of the Pterosporeae are in large part merely the characters of Arbutoideae; only saprophytism and the habit

TABLE 1. CHARACTERS OF NORTH AMERICAN MONOTROPEAE

Genus	Habit	Color	Flower	Placentation	Lobing of stigma	Fruit	Inner surface of ovary	Stele in stem
<i>Pterospora</i> . . .	tall, erect	pale purplish red	5-merous sympetalous	axile below, parietal above	obscure; opposite petals	loculicidal capsule	two layers of fiber-like cells	ring of bundles with lignified sheath
<i>Sarcodes</i> . . .	stout, erect, moderately tall	red	5-merous sympetalous	axile below, parietal above	opposite petals	capsule opening about base of style	scant differentiation near line of dehiscence	cylinder without sheath
<i>Alloctropa</i> . . .	tall, erect	white with red stripes	5-merous choripetalous asepalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of fiber-like cells	cylinder with sheath
<i>Monotropsis</i> . . .	slender, rather short, declined when young	white ?	5-merous sympetalous	parietal	obscure	berry	one layer of non-lignified elongate cells	ring of bundles, no sheath
<i>Hypopitys</i> . . .	slender, rather short, declined when young	white to yellow	4-merous choripetalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of non-lignified elongate cells	ring of bundles, no sheath
<i>Pityopus</i> . . .	slender, rather short, erect	white	4-merous choripetalous	parietal	obscure	berry?	undifferentiated	cylinder without sheath
<i>Monotropa</i> . . .	slender, rather short, declined when young	white	5-merous choripetalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of non-lignified elongate cells	ring of bundles with lignified sheath
<i>Pleuricospora</i>	small, erect, flowering at ground level	white	4-merous choripetalous	parietal	opposite sepals	berry	undifferentiated	cylinder without sheath
<i>Hemitomes</i> . . .	small, erect, flowering at ground level	pale yellow-pink	4-merous sympetalous	parietal	opposite sepals, petals, and stamens	berry?	undifferentiated	cylinder without sheath



TABLE 1, CONTINUED

Genus	Stele in pedicel and receptacle	Stamen bundles	Ovary wall bundles	Placentals	Style bundles	Anthers and pollen sacs	Dehiscence of anthers	Number of grooves on pollen grains
<i>Pterospora</i> . . .	cylinder	outer whorl fused to petal bundles, inner to carpel laterals	carpel laterals	in planes of petals; each is fused ventrals of same carpel	none	horizontal; dorsal sacs are longer	(1) proximal ends of lobes; (2) lengthwise of sides of lobes	4
<i>Sarcodes</i> . . .	ring of about 5 bundles	outer whorl fused to petal bundles, inner to ovary wall bundles	numerous; no definite carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	placentals	inverted; dorsal sacs are longer	proximal ends of lobes	4
<i>Allotropa</i> . . .	cylinder	outer whorl fused to petal bundles, inner free	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	erect when young, inverted when mature; dorsal and ventral sacs subequal	proximal ends of lobes	3
<i>Monotropis</i> . . .	about 4 partially fused bundles	two whorls, free of other bundles	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	horizontal when young, mature inverted; dorsal and ventral sacs subequal	proximal ends of lobes	2
<i>Hypopitys</i> . . .	flattened cylinder	two whorls, free of other bundles	carpel dorsals	in planes of sepals; fused or unfused ventrals of adjacent carpels	carpel dorsals	horizontal, ventrals sacs longer?	proximal ends of lobes?	2

TABLE 1, CONCLUDED

Genus	Stele in pedicel and receptacle	Stamen bundles	Ovary wall bundles	Placentals	Style bundles	Anthers and pollen sacs	Dehiscence of anthers	Number of grooves on pollen grains
<i>Pityopus</i> . . . .	cylinder	two whorls, inner connected to pistil bundles	8 carpel dorsals alternating with stamens	8, in planes of stamens	carpel dorsals	horizontal, ventral sacs longer?	proximal ends of lobes?	2
<i>Monotropa</i> .	ring of ten bundles	two whorls, free of other bundles	carpel dorsals	in planes of sepals; unfused ventrals of adjacent carpels	carpel dorsals	horizontal, ventral sacs longer?	proximal ends of lobes?	3
<i>Pleuricospora</i>	cylinder	outer whorl fused to petal bundles, inner free	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	vertical, dorsal and ventral sacs subequal	lengthwise of sides of lobes	4
<i>Hemitomes</i> . . .	broken cylinder	apparently one whorl; free of other bundles	8 carpels dorsals alternating with stamens	8, in planes of stamens	carpel dorsals	apparently vertical, dorsal sacs broader	dorsal sides of dorsal sacs	2



which is presumably a result of it are distinctive. Furthermore, the Pterosporeae are notably heterogeneous in anatomy of stem and receptacle, and in corolla, anther, fruit, and seed. I would allow the tribe to stand as a tentative group, and would expect studies of the Arbutoideae to afford evidence as to whether or not it is a natural group, having one origin among Arbutoideae.

The Monotropeae, though differing among themselves in various features, yet exhibit marks of unity; the saccate bases of the petals and the paired lobes of the nectary are associated with a peculiar and definite structure of the vascular supply to the petal. This is safely a natural group. In the corolla, *Monotropsis* is the most primitive of the genera; but in the ovary, *Hypopitys* and *Monotropa* are more primitive, and the feebly developed sheath of fibers is a primitive character in the stem of *Monotropa*. We may take it that in most respects *Monotropsis* represents a direct ancestor of *Hypopitys*, and *Pityopus* an only slightly modified descendant; *Monotropa* stands apart from all three, differing not only in the well known solitary flower and in the anatomy of the stem, but also in the number of grooves on the pollen grain. We may safely maintain *Hypopitys* and *Monotropa* as separate genera.

The tribe Pleuricosporeae has ceased to be tenable as constituted. The common characters of *Pleuricospora* and *Hemitomes*, in habit, floral diagram, placentation, and ovules, are features all of which are apparently readily reached by parallel change and some of which are widely distributed. They are outweighed by the differences in pubescence, vascular anatomy of the receptacle, and structure of the anther.

*Pleuricospora* is strictly glabrous. The petal bundles, not forking into two large bundles and one small one, are those of Pterosporeae rather than of Monotropeae. The anther is unique; the only thing elsewhere in the group that suggests it is that of *Pterospora*. The four-grooved pollen grains again suggest Pterosporeae rather than Monotropeae. But we cannot connect this genus with any one genus of Pterosporeae.

*Hemitomes* has the floral diagram of *Hypopitys*, and, in more extreme form, the irregularity of inflorescence observed in that genus. We may account for the unique petal trace of two bundles by supposing the small middle bundle of the petal traces of the Monotropeae to have been suppressed, this suppression being associated with loss of saccate bases to the petals and pairing of the lobes of the nectary. The slits along the dorsal sides of the dorsal sacs of the anthers seem to amount to a modification of the pores of normal Ericales, which are still present in *Monotropsis* and *Monotropa*. The two-grooved pollen grains are those of most Monotropeae.

It would be possible to dispose of these genera by assigning one to Pterosporeae, the other to Monotropeae, distinguishing these tribes by glabrous stamens and pistils in the former, pubescent stamens and pistils in most of the latter. Such a scheme,

however, would increase the heterogeneity of the Pterosporeae and break the unity of the Monotropeae. I think it best to place each of these genera in a separate tribe, making altogether four tribes to be distinguished as follows (the oriental genus *Cheilotheca* remains unplaced; it may perhaps constitute a fifth tribe):

- A. Stamens and pistils glabrous; lobes of the nectary not paired; no gaps above the petal bundles, to which the outer whorl of stamen bundles are more or less fused; grooves on the pollen grain 4 (3 in *Allotropa*); young stems not nodding.
  1. Stems erect above ground; red pigment present; anther bent inward; placentation axile below: Tribe PTEROSPOREAE: *Pterospora*, *Sarcodes*, *Allotropa*.
  2. Inflorescence at ground level; red pigment absent; anthers erect; placentation parietal: Tribe PLEURICOSPOREAE: *Pleuricospora*.
- B. Stamens and pistil often pubescent; red pigment usually absent (present in varieties of *Monotropa*, a trace of it in *Hemitomes*); gaps present above the petal bundles; grooves on the pollen grain 2 (3 in *Monotropa*).
  1. Bases of petals saccate; lobes of the nectary in pairs; petals with small dorsal bundles and large lateral bundles; young stems nodding (unknown in *Pityopus*): Tribe MONOTROPEAE: *Monotropsis*, *Hypopitys*, *Pityopus*, *Monotropa*, *Monotropastrum*, *Wirtgenia*?
  2. Base of petals not saccate; lobes of the nectary evenly distributed; dorsal bundles of the petals suppressed; inflorescence at ground level: Tribe HEMITOMEAE: *Hemitomes*.

Sacramento Junior College,  
Sacramento, California,  
August, 1940.

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## PODOCARPUS GRACILIOR IN CULTIVATION

JOHN T. BUCHHOLZ

The "African fern-pine," in recent years popular as a decorative tub plant and also planted in the open as an ornamental conifer, may become a tree of considerable size. Since mature specimens growing in California have produced pollen cones during the past winter, it is now possible to identify the species as *Podocarpus gracilior* Pilger.

The plant has been regarded as a conifer of South African origin and has usually passed under the nursery trade name of "*Podocarpus elongata*," which is unquestionably an error. The latter is the legitimate name of a plant of South Africa where there are two narrow leaved species that have been confused and have at one time or another passed under this botanical name. The California exotic has narrow leaves that are somewhat similar to those of *Podocarpus elongatus* L'Herit. (the earliest described

species in this genus), but the pollen cones and seeds differ considerably. It resembles *P. falcatus* (Thunb.) R. Br. (*P. elongata* Carr.) more closely than *P. elongatus* L'Herit., but has green instead of brown twigs, leaves that become longer and wider, and pollen cones that are more than twice as long; also the tips of individual microsporophylls (connectives) of the pollen cones are more pointed. In both *P. gracilior* and *P. falcatus* the pollen cones are axillary, borne singly or in fascicles of two or three.

The seeds of *Podocarpus gracilior* were brought over from East Africa in 1911 by Mrs. Stewart Edward White. Franceschi, of Santa Barbara, germinated some, if not all, of these. The statement is usually current that these seeds were introduced from South Africa (an error which has appeared in print), but the material itself does not agree with the descriptions of either of the narrow-leaved South African podocarps. It fits very closely the description of *Podocarpus gracilior*. This entire question has been clarified recently by a letter received from Colonel Stewart Edward White in which he states that the tree from which these seeds were collected was located in Kenya, British East Africa. This region of Africa is included in the range given for *Podocarpus gracilior* Pilger. Specimens of this species at the United States National Herbarium were collected in Kenya by Edgar A. Mearns of the Smithsonian African Expedition which was led by Theodore Roosevelt in 1909-1910. The male flowering material collected in California in January and February, 1941, in three widely separated localities agrees in all essential details with the Mearns specimens.

*Podocarpus gracilior* is dioecious, as are nearly all species of *Podocarpus*. Except for the limited number of original seedlings, the trees in California have been propagated from cuttings. The stock tree used for propagation since about 1922 at the Coolidge Rare Plant Garden Nursery in Pasadena is a male tree. During the past winter Mr. J. J. Mulvihill has kindly sent me a number of reproductive twigs. Thousands of plants have been grown as cuttings from this tree over a period of years and furnished to the nursery trade under the names "African Fern-Pine" and "*Podocarpus elongata*." They do very well as tub plants and when these long-suffering decoratives become too old they may be transplanted to parks and gardens. The writer has seen this conifer used as a street tree in Los Angeles and Pasadena. Apparently they do not become reproductive until they are mature specimens of large size. The largest known specimen, about fifty feet high, is growing at Alameda Plaza in Santa Barbara where two other mature specimens may be seen, none of which had been observed in reproductive condition. However, during July, 1941, Mr. Van Rensselaer of Santa Barbara Botanic Garden found one of these (located in the east section of Alameda Plaza) bearing seeds. Many of the seeds were abortive when less than half grown; some

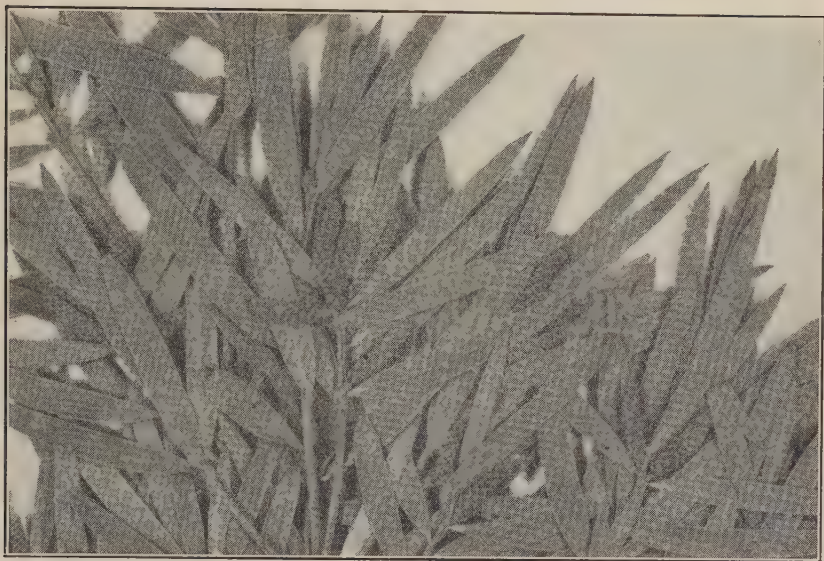


FIG. 1. Twigs of *Podocarpus gracilior* Pilger bearing nearly full grown pollen cones, January, 1941.

had enlarged to full size, but all of those which were examined by the writer, were without embryos, with the endosperms shriveled in the manner usual for unpollinated parthenocarpic seeds.

With this one exception, all reproductive specimens of *P. gracilior* thus far observed have proved to be male, although presumably the seeds would produce equal numbers of male and female seedlings. The location of many of the original seedlings is not known. Two specimens growing on the estate of Colonel Stewart Edward White near Burlingame have not been observed in reproductive condition at any time. The three large trees at Alameda Plaza are probably seedlings, and likewise any other old specimens growing in Santa Barbara. It is likely that the tree belonging to Mrs. E. N. Hazard, mentioned by Van Rensselaer (*Trees of Santa Barbara* 1940, p. 84) is also one of the original seedlings. In 1936 the writer found five or six large specimens on the Dwight Murphy estate at Montecito, Santa Barbara County and these may be seedlings. They have not been observed in reproductive condition.

The late Miss Kate Sessions of San Diego informed the writer in 1936 that she had obtained three of the original seedlings from Franceschi. The location of two of them was given. One is growing in the gardens of Julius Wangenheim, 148 West Juniper Street, San Diego. Another is the large tree at the Rosecroft Gardens in San Diego. The latter plant was not reproductive in



1936, but was found with pollen cones during the past winter. Mr. A. D. Robertson furnished the writer with male reproductive specimens from this plant in January and February, 1941.

A male tree growing in the Botanical Garden of the University of California, Berkeley, was observed to be in reproductive condition in January, 1941, by Mr. Donald G. Nelson of that institution. The origin of this plant is not known to the writer. Aside from the dozen plants enumerated here, there are probably a number of other specimens in cultivation on private estates that represent original seedlings, which were distributed in the days before it was discovered that these plants are easily propagated.

University of Illinois, Urbana,  
July 21, 1941.

## THE TAXONOMIC STATUS OF MICROSTERIS GREENE

HERBERT L. MASON

Perhaps no member of the Polemoniaceae has been so greatly misunderstood as the very polymorphic aggregate species, *Phlox gracilis* (Dougl.) Greene. It has been variously treated as a member of the following genera: *Gilia*, *Collomia*, *Phlox*, *Navarretia*, *Polemonium*, and is the type species of the genus, *Microsteris* Greene; it has been divided and subdivided into species, subspecies, varieties, subvarieties and forms within these genera according to the particular whim of the author treating it. The plant ranges from the Pacific Coast to the Rocky Mountains and from temperate Alaska south to Mexico, and recurs in the Southern Hemisphere in Bolivia, Chile, and Argentina. Essentially an early spring annual, it occurs from the coastal bluffs to timberline. The intent of the present paper is to deal only with the generic position of the aggregate species and not to be concerned with the status and disposition of the smaller taxonomic units. Therefore, the entire group of variants will be treated, for the present at least, as one large, polymorphic species.

The species was first collected by Douglas on the banks of the Spokane River [Washington] and given the manuscript name, *Collomia gracilis*; it was first described by Hooker (6) in 1829 under the name *Gilia gracilis* with *Collomia gracilis* Douglas cited as a synonym. In 1887 Greene (4) referred the species to the genus *Phlox* with the statement: "This interesting plant came to the knowledge of botanists some years in advance of *Phlox Drummondii* Hook. and its allies. It was at first a thing of dubious aspect, not at home either in *Gilia* or *Collomia*. But since the discovery of the Texan group of annual species of *Phlox* with peculiar habit, it must have been the mere force of custom which has kept men from seeing that it is an absolutely perfect congener of *Phlox Drummondii*." In 1891 (7, p. 433) O. Kuntze, recognizing the page priority of *Navarretia* over *Gilia*, made a purely nomencla-

torial shift in the combination *Navarretia gracilis* (Dougl.) Kuntze. In 1898 Greene (5) erected the genus *Microsteris* recognizing as species seven segregates of *Phlox gracilis*. In so doing Greene stated: "At present I am disposed to adopt it as a principle that species with mucilaginous seeds are nowhere, in this family, to be placed as congeneric with such as have seeds devoid of the gum-miferous coating. This implies the removal of my *Phlox gracilis* from the genus *Phlox*." In his description of *Microsteris* he states "Calyx, corolla, stamens and capsule wholly as in *Phlox*." Thus Greene's *Microsteris* hangs by the single character "mucilaginous seeds." In the same year O. Kuntze (8, p. 203) referred *Collomia gracilis* Dougl. to *Polemonium* by the simple statement: "*P. Morenonsis* OK (*Collomia gracilis* Dgl. non *Polemonium gracile*)."  
His reasons are forever hidden in parenthetical synonymy. We can dismiss without further comment the references to *Navarretia* and *Polemonium*. The reference by Douglas to *Collomia* is understandable. It was based upon superficial resemblance; furthermore, at that time the genus *Collomia* had not been clearly circumscribed in the light of the family as a whole. Our problem resolves itself into determining whether *Phlox gracilis* shall be retained in *Gilia* as interpreted by Hooker, be retained in *Phlox* as interpreted by Greene in 1887 or be placed in *Microsteris* following Greene's later interpretation. Of subsequent authors most have preferred to follow Asa Gray's adaptation of Hooker's treatment in a broad concept of the genus *Gilia* while only a few have used either *Phlox* or *Microsteris* when referring to this species. Brand (2) in his monograph of the Polemoniaceae with its highly elaborated system of "pigeon holes" chose to place *Phlox gracilis* in the genus *Gilia*, subgenus *Benthamiophila*, section *Phlogastrum* and proceeded to divide the species into fourteen entities in various sub-specific categories. With respect to the generic position of the species I quote from Brand, "Species sic intermedia inter genera *Phlox* et *Gilia*, ut vix discernere possis, cui generi eam attribuas; a *Collomia* tamen, quacum plurimi autores junxerunt, calyce, ut cl. Greene docuit, valde diversa." Although he cited *Microsteris* as a synonym it is clear from the above quotation that he did not regard *Microsteris* as offering any problem. He was concerned with differentiating *Gilia* from *Phlox*. Here again we find but a single character utilized to place the species in *Gilia*, namely, the fact that the seeds develop mucilage when wetted. Other characters which it possesses that align it with *Phlox* are treated by Brand as exceptions in *Gilia*.

The most recent treatment that bears on this problem is that of Wherry (9) from whom we quote, "*Microsteris*. A few diminutive western annuals constitute this genus, which has been by various authors referred to *Collomia*, *Gilia* and *Phlox*. It shows little relationship with the first two genera, and in view of the difference in seeds can scarcely be congeneric with the last, although it may well be a derivative." Wherry, it will be seen, dismisses

*Gilia* and *Collomia* from consideration but parries between *Phlox* and *Microsteris*. He finally eliminates *Phlox* on the basis of "COROLLA-LIMB small; seeds becoming sticky when moistened," but he does at least suggest the responsibility of *Phlox* for the offspring. In an effort to validate the genus *Microsteris* another very insignificant character is added to the one previously utilized, namely the small size of the corolla limb.

It is perhaps a reasonable mode of escape when a group of plants does not fit comfortably in any of the related genera to erect a genus for it. However, this procedure should not be adopted until all of the evidence is carefully weighed to determine the precise nature of the differences that seem to make it necessary. As pointed out above *Microsteris* was erected by Greene who listed for it a single character difference from *Phlox*. Wherry's additional character of a small corolla limb adds scarcely anything of generic significance. The following tabular arrangement presents the facts pertaining to the development or non-development of mucilage or spiracles in the seed coats of most of the more widely accepted genera or Polemoniaceae.

*Bonplandia*: all species develop mucilage.

*Cantua*: a few species develop spiracles, the rest do not.

*Cobaea*: some species produce spiracles, and other species mucilage.

*Gilia*: very diverse, some species produce mucilage, others do not. The section *Ipomopsis*, recognized as a distinct genus by Wherry, is about equally divided in this respect.

*Hugelia*: some species produce mucilage, others do not.

*Langloisia*: all species produce mucilage.

*Leptodactylon*: in species examined none produce mucilage.

*Linanthus*: most species produce mucilage, some do not.

*Loeselia*: some produce mucilage, others do not.

*Navarretia*: some produce mucilage, others do not.

*Phlox*: as interpreted by Greene and by Wherry, does not produce mucilage, but if *Microsteris* is included, will be on the same basis as the other large genera.

*Polemonium*: some species produce mucilage, others do not.

The remaining few genera are each very small, and I have not as yet investigated them. But from the above data it would appear that the development of mucilage by the seed coat cannot be relied upon as of primary generic significance. All we can say of *Phlox* is that in the majority of species the seeds are immutable when wetted. This leaves as a character for the segregation of *Microsteris* only the small corolla limb. The magnitude of difference here, however, is no greater than the variational limits of corolla size in several other genera of Polemoniaceae, such as *Collomia*, *Navarretia* and *Linanthus*. This evidence, it seems, is just cause for denying generic status to *Microsteris*.

When we consider the characters that serve to keep the *Phlox gracilis* aggregate out of *Gilia* we turn from the flower and seed to





PLATE 12. COMPARISON OF PHLOX GRACILIS AND PHLOX DRUMMONDII VAR. TENUIS. FIG. 1. *Phlox gracilis*. FIG. 2. *Phlox Drummondii* var. *tenuis*. FIG. 3. *Phlox gracilis*, flower. FIG. 4. *Phlox gracilis*, opened corolla. FIG. 5. *Phlox gracilis*, capsule showing disarticulation of valves. FIG. 6. *Collomia*, capsule showing valves with margins reflexed. FIG. 7. Campanulate type of capsule found in many species of *Linanthus* and *Gilia*.

other parts of the plant. Of the authors who have referred the group to *Gilia* we find some who regard most of the small genera (*Linanthus*, *Hugelia*, *Gymnosteris*, *Loeselia*, *Collomia*, *Leptodactylon*) as belonging to this genus; others who recognize the small genera mentioned above but who have followed precedent in the disposition of *Phlox gracilis*. When we exclude from *Gilia* these small genera there still remains a polymorphic but closely related group of species. The leaves of this remaining group are normally alternate (occasionally through shortening of the internodes they may appear subopposite), and frequently pinnately toothed, lobed or dissected; the corolla lobes are normally entire; the stamens are usually, but not always, equally inserted and equal in length; the capsule valves do not disarticulate on dehiscence but remain united at the base, and although the valves may spread campanulately or sometimes reflex on the midvein the capsule falls as a whole (pl. 12, fig. 7); the locules of the ovary are usually more than one-seeded, but occasionally are one-seeded; the seeds are usually small and angular.

*Phlox gracilis* does not conform with *Gilia* as the following summary of its characters demonstrates: the leaves are predominately opposite (pl. 12, fig. 1), at least below, and are always linear, or oblong and entire; the corolla is salverform, the limb rotate, the lobes frequently emarginate (pl. 12, fig. 3); the stamens are unequally inserted and unequal in length (pl. 12, fig. 4); the capsule valves are rigid and disarticulate completely on dehiscence; the locules are one-seeded, the seeds large (pl. 12, fig. 5). Greene was quite correct when he said in his diagnosis of *Microsteris*, "Calyx, corolla, stamens and capsule wholly as in *Phlox*." And of course Wherry accepts for this group a close relationship to *Phlox*. It seems that the presence of such typical *Phlox* characters as the rigid, disarticulating capsule valves and the solitary large seeds in the locules, together with several minor characters which are usual in *Phlox* and occasional or abnormal in *Gilia*, throw the weight of the argument to *Phlox*, not to *Gilia*.

Another line of evidence supporting a relationship with *Phlox* rather than with *Gilia* is found in cytological studies; the basic chromosome number in *Gilia* appears to be  $n=9$  while the basic chromosome number in *Phlox* is  $n=7$ . In *Phlox gracilis*  $2n=14$ , the count being made from root tip cells. However, in a group with such wide climatic tolerance and such great morphological diversity we may anticipate some polyploidy.

Botanists familiar with the genus *Phlox* only in western North America may be pardoned for hesitating to place *P. gracilis*, a plant so different from *P. Douglasii* and *P. adsurgens*, in the same genus. It is, as Greene points out, only when we take into consideration the range of variation of the entire genus that we can hope for a true picture of relationship. In this case the *Phlox Drummondii* complex of Texas offers a key to the relationship. A collection of *Phlox Drummondii* var. *tenuis* Gray from Texas

(*Lindheimer 468*) is an excellent example of a connecting type between *Phlox gracilis* and other members of the genus. A comparison of figures 1 and 2 (pl. 12) will at once show the great similarity in aspect between the two. Figure 1 represents a plant of *Phlox gracilis* collected at Tuolumne Meadows, Yosemite National Park, California (*Mason 4869*). It was especially selected for this comparison but is representative of a large segment of the "*Microsteris*" variants. The evidence of a general similarity of aspect substantiated by indisputable *Phlox* characters upholds Greene's first opinion of the generic position of this group.

The fact that this western group of plants is related to an eastern group by way of a southern bond is not inconsistent with the growing body of information now being accumulated relative to the history of vegetation in the southwest. Among other genera with related species showing a similar distribution pattern are *Juglans*, *Cercis*, *Forestiera* and *Fraxinus*. This group of trees and shrubs are all represented in fossil floras of Middle Tertiary time and today occur in savanna like floras where *Phlox gracilis* is a common associate. It would seem that these relationships go back at least as far as the Miocene, if not the Oligocene, in the Sierra Madrean flora of Axelrod (1). Perhaps this region has been the center of origin and differentiation of the entire Polemoniaceae. Certainly not all *Phlox* species have had their origin in Keewatin Land as postulated by Wherry (10). If this were true it would be reasonable to expect a higher development of the genus in the old world than is now evident, since migration routes through Beringia would have been available. The occurrence of *Phlox* in this northern region during the Pleistocene, north and west of the Keewatin center of glaciation is attested by fossil fruits reported and figured by Chaney and Mason (3 p. 17, figs. 34, 36). These specimens are strikingly similar to *P. sibirica* L., a species occurring in the Alaska region today, and ranging westward into Siberia.

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of California, Berkeley,  
August 27, 1941.

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## THE HOLACANTHOID PLANTS OF NORTH AMERICA

CORNELIUS H. MULLER

One of the striking botanical phenomena of the southwestern United States and adjacent Mexico is the occurrence of several genera of different families with vegetative characters so similar as to make them confusing. Perhaps the most outstanding such instance is that of the usually leafless green spiny shrubs which resemble *Holacantha Emoryi* A. Gray, a member of the Simarubaceae. The similar forms are *Koeberlinia spinosa* Zucc. in the Koeberliniaceae, *Canotia holacantha* Torr. in the Celastraceae, and *Thamnosma montana* Torr. & Frem. in the Rutaceae.

These four species are characterized by leaves reduced to scales and early caducous, and spinescent stems persistently green to carry on the photosynthetic process. The lack of leaves and similarity of the spines make these plants rather difficult to distinguish without flowers or fruit. Yet, a series of vegetative characters may be recognized by which the species are readily distinguished.

There are other spinescent plants which might be confused with the group here treated. The others, however, are characterized by shorter and more slender spines and usually more prominent leaves. For instance, *Adolphia* in the Rhamnaceae and *Forsellesia* in the Celastraceae contain species highly similar in habit to the *Holacantha*-like plants, but in these the spines do not exceed an average of 2.5 millimeters in thickness, and the leaves are prominent throughout the greater part of the growing season. Furthermore, *Adolphia* is characterized by opposite leaves and branches, while those of the plants here treated are all alternate. Two variants of *Koeberlinia spinosa* have been distinguished under varietal names. Both of these are characterized by very slender spines which might make them difficult to distinguish from *Adolphia* except for their alternate habit of branching. Leafless individuals of the leguminous shrubs *Cercidium* and *Cassia armata* might become confusing when they lack flowers and fruit.

The highly artificial group comprised of the *Holacantha*-like plants is characterized by the alternate-branching, spinescent stems, the spines usually quite coarse, branches green and photosynthetically functional for several years, leaves much reduced and early caducous. Johnston (Journ. Arn. Arb. 21: 356-363, 1940) has pointed out the significance of this group of unrelated plants of similar habit as indicative of a relationship between the North American deserts and those of South America where the same habit is common. He showed the habit to be much more general in the South American deserts than in North America. The highly endemic character of all our species except *Koeberlinia spinosa* would indicate that the plants are relicts of a time when the habit was more common in North American deserts.

## KEY BASED ON VEGETATIVE CHARACTERS

Leaf scars and branching alternate, leaves inconspicuous and early caducous.

Plants glabrous, stem either densely glandular or with minute longitudinal lines of white waxy flakes.

Stems densely glandular or warty with translucent glands; buds and spine tips tan; branches with a pair of extra-axillary buds at the bases (one on each side) . . . . . *Thamnosma*

Stems not glandular, with minute longitudinal lines of white waxy flakes; buds dark brown or black, spine tips brown; branches with no extra-axillary buds at the bases (though the buds along the length of the branch may descend to a point near the base) . . . . . *Canotia*

Plants with young stems pubescent, neither glandular nor with waxy exudations.

Younger stems yellow-green, minutely puberulent with short spreading hairs or these reduced to pustules; branches and spines with a pair of buds at the bases, these extra-axillary (one on each side) . . . . . *Koeberlinia*

Younger stems gray green with densely matted appressed silky hairs; branches and spines with a single axillary bud and no lateral or extra-axillary buds at the bases . . *Holacantha*

Leaf scars and branching opposite or, if alternate, the leaves conspicuous and persistent . . . (genera not treated in this article).

*THAMNOSMA MONTANUM* Torr. & Frem. in Frem., Rep. Exped. Rocky Mts. 313. 1845.

Central Arizona north to southwestern Utah, southern Nevada, and southern California; most common in western Arizona. A shrub usually 3 to 6 or 7 decimeters tall. (fig. 1).

*CANOTIA HOLACANTHA* Torr., U. S. Rep. Survey Railroad Miss. Pac. 4: 68. 1856.

Southeastern and central Arizona to northwestern Arizona and doubtfully in the Providence Mountains of southeastern California. A shrub 3 to 5 or even 6 meters tall. (fig. 2.)

*KOEBERLINIA SPINOSA* Zucc., Abh. Akad. Muench. 1: 359. 1832.

Southern Arizona and New Mexico, western Texas, Baja California, northern Sonora and Chihuahua, south through Coahuila and Nuevo Leon to Puebla and Oaxaca. A shrub 0.5 to 2 meters or even a small tree to 5 meters tall. (fig. 1.)

*KOEBERLINIA SPINOSA* var. *TENUISPINA* Kearney & Peebles, Journ. Wash. Acad. Sci. 29: 486. 1939.

Yuma County, Arizona, and Sonora, Mexico. Differs from the species in its elongate slender spines, blue-green color, and usually longer sepals, petals, and filaments. Typical *K. spinosa* apparently occurs nowhere west of Tucson, Arizona. This variety is not distinguished from the species on the distribution map.

A second variety (*K. spinosa* var. *verniflora* Bogusch, Torreya 31: 74. 1931) now scarcely seems worthy of distinction. Although this form differs strikingly from the species by its slender spines (and generally reduced size of the organs) and its early flowering (in March and April), its differences are not sufficiently profound nor constant to warrant formal recognition. Nor is



FIG. 1



FIG. 2

Figs. 1 and 2. Distribution of holcanthoid plants in southwestern North America.



there any geographical segregation from the species. The morphological basis of this form has been observed by the author in various parts of western Texas and adjacent Chihuahua and Coahuila. In a letter to the author under the date October 7, 1940, Bogusch discusses the variety as follows: "... observations made in the field upon specimens of *Koeberlinia spinosa* Zucc. convince me that the variety *verniflora* described by me is probably a normal reaction of the plant to wound stimulus or represents a form of juvenile growth. From material seen both in the type locality of the Rio Grande Valley of Texas and in the region west of Uvalde, I have seen that new growth which follows extensive injury to the plant often results in being more attenuated, both in branches and the spines. The peculiarities associated with the time of flowering—not necessarily a taxonomic character—may be best explained that in the Rio Grande Valley the vegetation in many respects matures earlier and comes into flower sooner than elsewhere in the state."

*HOLACANTHA EMORYI* A. Gray, Mem. Am. Acad. ser. 2, 5 (Pl. Nov. Thurb.): 310. t. 8. 1855.

Central and southwestern Arizona to southern California. A shrub 1 meter tall to a small tree reaching 3.5 meters (fig. 2).

An undescribed species of *Holacantha* was recently discovered in northern Mexico.

*Holacantha Stewartii* sp. nov. Frutex procumbens vel ascendens 1.5–3(6) dm. altus duplo latior; spinae plusminusve appresso- vel patenti-pubescentes glabratae, papillis minutis exceptis; fructus acutus margine ventrali obtuso-costatus.

Low shrub, 1.5–3 dm., rarely 6 dm. tall, usually 2–4 times as broad, procumbent or somewhat ascending, soon leafless, coarsely spiny; stems and spines divaricate; spines 2.5–6(12) cm. long, (1.5)2.5–3 mm. thick, tips subulate, brown, 3–4 mm. long, branches terete, the immature ones becoming sulcate in drying, glabrate or somewhat spreading-pubescent or appressed-sericeous, hairs short, bases persisting as minute papillae; buds inconspicuous in axils of spines and sparsely scattered along their length, surrounded by small tufts of coarse appressed hairs; leaves quickly deciduous, oblong, acute at both ends, sessile, 5–8 mm. long, 2–2.5 mm. broad, red at veneration (as are the young spines for a time), densely white- or rose-hirsute, becoming green and sparsely hirsute; flowers dioecious; staminate calyx of 6 ovate, acute, pubescent sepals about 1 mm. long; corolla of 6 fleshy, dorsally pubescent, deeply concave petals with narrow, thin margins, 4 mm. long, 1.75 mm. broad (not flattened), stamens about 12, filaments 1.5–2 mm. long, broadened basally, strongly hirsute, apex subulate, glabrous; pistillate calyx similar to the staminate; pistillate corolla not seen; staminodes similar to the functional filaments; carpels distinct, apically connivent, stigmas sessile, fused; fruit persistent 1–2 years, 6-carpellate (or carpels fewer

by abortion), carpels distinct, divaricate, lenticular-ovate, acute, ventral margins obtusely ridged, superior, 8–9 mm. long, 5–6 mm. broad, 3–4 mm. thick, glabrous, red or green, surface nearly smooth, lacquered. (fig. 2.)

Range: Mexico; western Coahuila and northern Zacatecas.

*Holacantha Stewartii* is named in honor of Mr. Robert M. Stewart of Santa Elena, Coahuila, whose superior hospitality and whose company on several side trips contributed markedly to the pleasure and success of the several weeks' work in the vicinity.

This species is the second described in this rare and striking genus, the first being *Holacantha Emoryi* which is confined to Arizona and California. From that species *H. Stewartii* differs in its low sprawling habit, the sparse pubescence of its stems (compared with the densely short-tomentose stems of *H. Emoryi*), the persistence of papillae-like hair-bases, and its usually markedly acute and ventrally ridged carpels. The great discrepancy in the ranges of these two endemics further attests their distinctness.

Specimens examined. COAHUILA: Sierra de las Cruces, gulch in limestone hills 0.5 mile north of Santa Elena, August 13, 1940, *I. M. Johnston & C. H. Muller 215* (United States National Arboretum, USNA, type, sheet no. 96733; Arnold Arboretum, AA); southeast base of Sierra de las Cruces, 3 miles northeast of San José, September 5, 1940, *I. M. Johnston & C. H. Muller 1003* (AA, USNA); north base of Sierra de las Cruces, at San Rafael, September 8, 1940, *I. M. Johnston & C. H. Muller 1034* (AA, USNA); northwest base of Sierra de las Cruces, at San Vicente, September 8, 1940, *I. M. Johnston & C. H. Muller 1065* (AA, USNA); 3 to 5 miles south of Laguna de Jaco, September 10, 1940, *I. M. Johnston & C. H. Muller 1104* (AA, USNA); north end of Bolson de los Lipanes between El Almagre and Cerros de Leja, September 12, 1940, *I. M. Johnston & C. H. Muller 1239* (AA, USNA). ZACATECAS: banks of arroyos in foothills, Hacienda de Cedros, 1908, *F. E. Lloyd 191* (United States National Herbarium).

With the exception of the type collection and Lloyd's from Zacatecas all the plants collected or observed grew in deep, heavy silt flats, usually associated with *Koeberlinia spinosa* Zucc. Although the most luxuriant growth and fruiting occurs in rocky arroyo sites, the species is obviously more at home in the former habitat, as is evidenced by its more frequent occurrence there. The plant is often the only one (or one of a few) on otherwise bare silt. Its procumbent habit serves to bind the soil and forms hillocks down the sides of which the branches sprawl.

In two of the seven collections studied fasciated stems were noted. These are flattened and falcate with two ranks of simple normal spines issuing from their edges. It is odd that two such cases of identical abnormality were encountered in so rare a plant, about fifty individuals being observed in the course of a wide and painstaking search.

Bureau of Plant Industry, Washington, D. C., February, 1941.

## COMBINATIONS PROPOSED IN "THE HIGHER PLANTS OF OREGON"

MORTON E. PECK

There has been some question as to the validity of certain new combinations proposed in the "Manual of the Higher Plants of Oregon," recently published by the writer. The citations required if one is to adhere strictly to the International Rules (Ch. 3, Sec. 6, Art. 44), are, therefore, published herewith. Numbers in parentheses refer to pages of the "Manual" on which the new combination was made.

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*BRODIAEA DOUGLASII* var. *Howellii* (Wats.) comb. nov. *B. Howellii* Wats., Proc. Am. Acad. Sci. 14: 301. 1879. (By error as *B. grandiflora* var. *Howellii*, p. 199)

*HABENARIA ELEGANS* var. *multiflora* (Rydb.) comb. nov. *Piperia multiflora* Rydb., Bull. Torr. Club 28: 638. 1901. (p. 219)

*ERIOGONUM OVALIFOLIUM* var. *ochroleucum* (Small) comb. nov. *E. ochroleucum* Small, Mem. N. Y. Bot. Gard. 1: 123. 1900. (p. 256)

*ATRIPLEX PATULA* var. *obtusata* (Cham.) comb. nov. *A. angustifolia* var. *obtusata* Cham., Linnaea 6: 569. 1831. (p. 267)

*LEWISIA COTYLEDON* var. *Howellii* (Wats.) comb. nov. *Calandrinia Howellii* Wats., Proc. Am. Acad. Sci. 23: 262. 1888. (p. 281)

*ARENARIA ACULEATA* var. *uintahensis* (Nels.) comb. nov. *A. uintahensis* Nels., Bull. Torr. Club 28: 7. 1899. (p. 286)

*SILENE OREGANA* Wats. var. *filisecta* comb. nov. *S. filisecta* Peck, Proc. Biol. Soc. Wash. 47: 186. 1934. (p. 296)

*ANEMONE GLOBOSA* var. *lithophila* (Rydb.) comb. nov. *A. lithophila* Rydb., Bull. Torr. Club 29: 152. 1902. (p. 309)

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Willamette University,  
Salem, Oregon,  
August 9, 1941.

## AN UNDESCRIBED SPECIES OF STIPA FROM CALIFORNIA

G. L. STEBBINS, JR., AND R. M. LOVE

Due to the growing interest in the native forage plants of California, particular attention is now being given by a number of workers to *Stipa pulchra* Hitchc., one of the most common and valuable of the native perennial forage grasses in the valley and foothill regions of this state. Several people, including the present writers, have noticed that this species as recognized in the current manuals actually consists of two distinct types. One, with deep green foliage, relatively broad leaves, stiffer panicle branches, large glumes, thick, fusiform lemmas, and stout, stiff awns, is predominant in the outer Coast Ranges and the wooded parts of the Sierra Nevada foothills. This is typical *S. pulchra*, of which the type came from Healdsburg, Sonoma County. The other form, with somewhat glaucous foliage, narrower leaves, flexuous, often nodding panicle branches, smaller, narrower glumes, slender lemmas, and slender, often flexuous awns, occurs chiefly in the treeless parts of the inner Coast Ranges, the San Joaquin Valley (in scattered areas undisturbed by cultivation), the valleys of southern California, and the edges of the deserts. The two types have been given different common names, typical *S. pulchra* being known as purple needle grass, and the slender, interior type as nodding needle grass. The writers have observed these two needle grasses carefully during two seasons of collecting in the field, have grown and compiled extensive morphological data on several cultures of each, and have examined their chromosomes at both mitosis and meiosis. From these observations enough evidence has accumulated to warrant the recognition of the interior type as a distinct species. It may be described as follows.

*Stipa cernua* sp. nov. Folia glauca angusta; panicula ampla, ramis tenuis, flexuosis, cernuis; glumae inaequales, 12-19 mm. longae, 1-1.4 mm. latae, pallidae vel roseo-purpureae, semper 3-nervatae; lemma angusta, 5-10.5 mm. longa, cum fructu 0.6-1



FIG. 1. Distribution of *Stipa pulchra* and *S. cernua*.

mm. crassa, ad basim et supra nervis pubescens, parte superiore glabra; arista 6–11 cm. longa, flexuosa, scabra vel ad basim pubescens.

Mostly in large clumps, the basal leaves numerous, narrow, usually glaucous; culms several, mostly 60 to 90 cm. tall, middle culm leaves 1.2–2.4 mm. broad. Panicle ample, the basal portion often within the lowermost leaf sheath; panicle branches slender and flexuous or cernuous; glumes scarious, pale or reddish purple, long acuminate, the lower 12–19 mm. long, the upper somewhat shorter and broader, 1–1.6 mm. broad, both strictly 3-nerved; lemma 5–10.5 mm. long, 2.2–2.9 mm. broad when unrolled, with caryopsis 0.6–1 mm. thick at maturity, 5- or sometimes 7-nerved, the callus acute, pubescence dense on the callus and on the lower

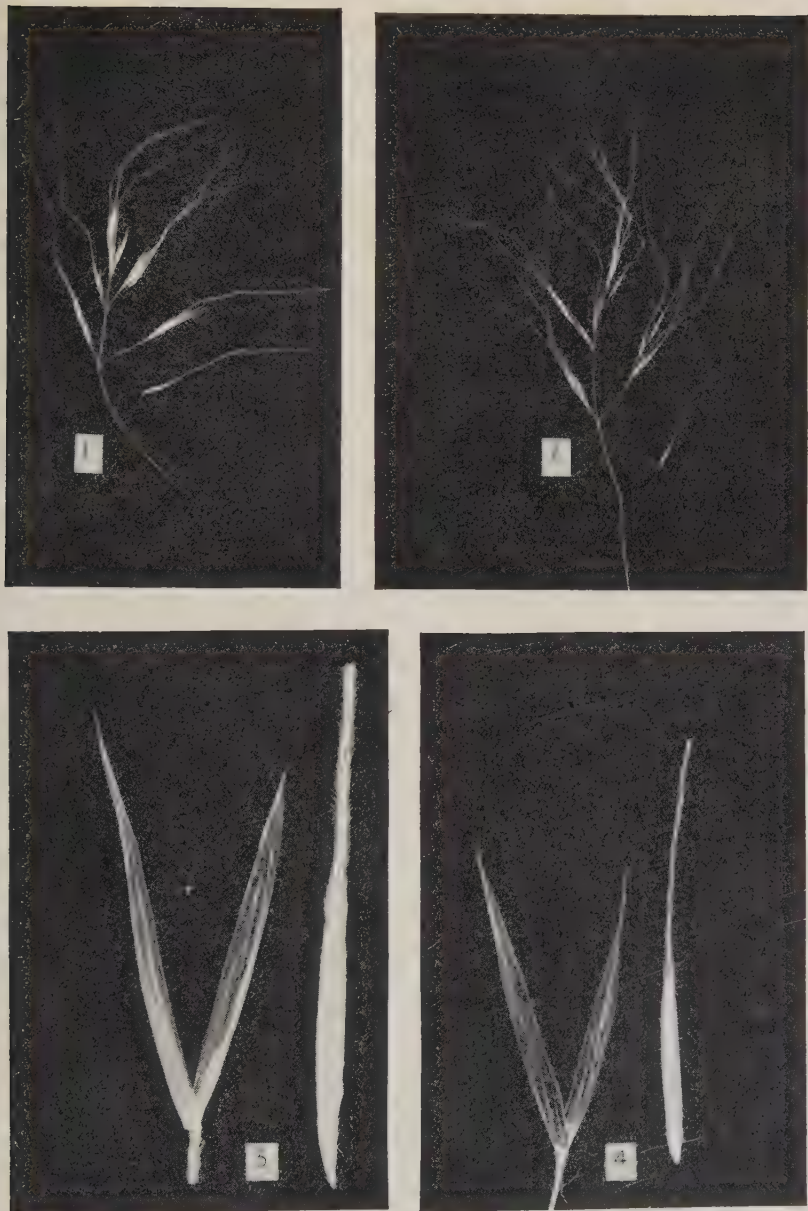


PLATE 13. INFLORESCENCE AND FLORETS IN STIPA. FIG. 1. *Stipa pulchra* Hitchc., from Berkeley (*Stebbins 2670*), panicle branch  $\times 33$ . FIG. 2. *S. cernua*, from Santa Barbara County (*Stebbins 2875*), panicle branch  $\times 33$ . FIG. 3. *S. pulchra*, from Berkeley, glumes and lemma  $\times 3.3$ . FIG. 4. *S. cernua*, type collection, glumes and lemma  $\times 3.3$ .



TABLE 1

Comparison of the Principal Characteristics of *Stipa pulchra* and *Stipa cernua*

	<i>S. pulchra</i>	<i>S. cernua</i>
Width of next to uppermost culm leaf .....	2.4-6 mm.	1.2-2.4 mm.
Color of leaves .....	deep green	glaucous
Character of panicle branches	spreading, or slightly cernuous	slender, flexuous, or cernuous
Length lower glume .....	15-26 mm.	12-19 mm.
Width upper glume .....	1.4-2.2 mm.	1.0-1.6 mm.
Number of nerves on upper glume .....	3-5	3
Length of lemma .....	7.5-13 mm.	5.0-10.5 mm.
Width of lemma (unrolled) .	3.3-4.8 mm.	2.2-2.9 mm.
Number of nerves on lemma	5-9	5-7
Thickness of mature caryopsis including lemma ....	1.0-1.4 mm.	0.6-1.0 mm.
Pubescence of lemma .....	throughout, or at base and on nerves to middle or summit	at base and on nerves one-third to four-fifths of way to summit
Length of awn .....	60-90 mm.	60-110 mm.
Ratio of awn to lemma .....	5.9-9.8	8.7-14.5
Pubescence of awn below first bend .....	pubescent	scabrous or slightly pubescent

one-fifth to one-fourth of the body of the lemma, the upper part of the lemma scabrous and with the nerves pubescent one-third to four-fifths of the distance to the summit, lemma usually pale straw- or buff-colored, occasionally purplish, brownish, or blackish; awn 6-11 cm. long, 8.7-14.5 times the length of the lemma, twice bent at maturity, slender and flexuous beyond the second bend, scabrous or short-pubescent below the first bend.

California, from Tehama County south to San Diego County east to the Sierra Nevada foothills, reaching the coast from Monterey southward, and extending up to about 1360 meters (4500 feet) altitude in southern California.

Type. West side of Cedar Mountain Ridge, southeast of Livermore, Alameda County, altitude 400 meters (1300 feet), *G. L. Stebbins, Jr. 2732*, (Herb. Univ. Calif. 641631). The following specimens in the University of California Herbarium are also typical: west of Orland, Glenn County, *Heller 11434*; Nacimiento River, Monterey County, *Davy 7688*; Santa Barbara, *Elmer 3874*; Mount Pinos, Ventura County, *Hall 6426*; Mint Canyon, east of Saugus, Los Angeles County, *Munz 6794*; near Rialto, San Bernardino County, *S. B. & W. F. Parish 2038*; San Bernardino Valley, *Parish 6204, 11257*; near Winchester, Riverside County, *Hall 2921*; Box Springs Mountain, Riverside County, *Hall 2977*; San Diego, *Brandegee 833*.

As mentioned previously, *Stipa cernua* is most closely related to *S. pulchra*. The differences between the two species are sum-

marized in Table 1, and partly illustrated in plate 13. The following may be used as convenient key characters:

- Leaves green, the middle culm leaves 2.4-6 mm. broad; lemmas fusiform, with caryopsis 1-1.4 mm. thick at maturity; awn stout and stiff, mostly 7-9 times as long as the lemma ..... *S. pulchra*
- Leaves somewhat glaucous, the middle culm leaves 1.2-2.4 mm. broad; lemmas slender, with caryopsis 0.6-1 mm. thick at maturity; awn slender, flexuous beyond the second bend, mostly 9-12 times the length of the lemma ..... *S. cernua*

The distribution of the two species, as determined by the collections and observations of the writers as well as by the specimens in the University of California Herbarium, is shown in figure 1. It will be seen that they occur together throughout a rather large area, and can often be found growing side by side. In these places they are usually quite distinct, but forms intermediate between them do occur. The writers studied particularly these intermediate plants as found in two localities near San Benito, San Benito County, and found them to be completely sterile or nearly so. Although the surrounding plants of *S. pulchra* and *S. cernua* were producing good seed in abundance, not a single fertile grain was found on any of the intermediates. The latter showed considerable hybrid vigor, often forming clumps much larger than those of the parent species. In the University of California Herbarium there are three specimens of such sterile intermediates: north base of Mount Hamilton, Santa Clara County, *Sharsmith 664A*; Pacific Grove, Monterey County, *Elmer 3507*; Las Flores Canyon, Santa Monica Mountains, Los Angeles County, *Epling* in 1930. Only the latter specimen had anthers with pollen for examination; in it 5 per cent of the pollen grains were large and well filled with cytoplasm, as contrasted with 90-96 per cent in typical *S. pulchra* and *S. cernua*.

The chromosome numbers of the two species are reported elsewhere as  $2n = 64$ ,  $n = 32$  for *S. pulchra*, and  $2n = 70$ ,  $n = 35$  for *S. cernua* (Stebbins and Love, *Am. Jour. Bot.* 28: 371-382. 1941). Three of the sterile intermediate plants from San Benito were dug up and transplanted to pots in Berkeley, and their somatic chromosome number was determined as  $2n = 67$ , indicating that they are actually first generation hybrids between *S. cernua* and *S. pulchra*. Their meiosis will be studied during the coming season.

Except for *S. pulchra*, *S. cernua* has no close relative among the North American species of *Stipa*. It resembles *S. comata* in its glaucous leaves and long awns, but that species has large, thick lemmas as in *S. pulchra*, and lacks the collar at the apex of the lemma which is found in both *S. pulchra* and *S. cernua*. It is possible that *S. cernua* is related to some of the numerous South American species of *Stipa*, but the present writers have not seen adequate material of any of them to judge their relationships.

College of Agriculture,  
University of California, Berkeley,  
January, 1941



## REVIEWS

*The Evolution of Land Plants [Embryophyta]*. By DOUGLAS HOUGHTON CAMPBELL. Pp. 1-731 with 351 text figures. Stanford University Press. 1940.

This large volume has two main elements. It is a résumé of the author's half century of morphological, chiefly embryological, study; and it is a condensed summary of the work of other writers on the relationships of the higher plants. Of these, the former is the more valuable, which is natural since Dr. Campbell has himself been the foremost contributor to our understanding of the broader lines of the evolution of the land plants. It is as to these broad lines, where the work of the past fifty years has brought confidence in some things and doubt as to others, that this book registers well the present state of science and can serve as a mile post.

The larger part of the book is taken up by the finer classification, to orders, families, in some places to genera. Here the author depends more upon the views of others, and the presentation is distinctly less authoritative. For example, among the ferns, the Eusporangiatæ are well presented, but the treatment of the higher Leptosporangiatæ is comparatively weak.

In accord with custom, the evidence of paleophytology is treated with respect. This science has of course made progress in various respects. But the reviewer would still recall a remark of Dr. Joseph Hooker. "Amongst the many collections of fossil plants that I have examined, there is hardly a specimen, belonging to any epoch, sufficiently perfect to warrant the assumption that the species to which it belonged can be recognized." Yet, specific characters may petrify better than those of classes. Consider spermatozoids and the embryo-sac. A discussion of the nature and value of evidence would be a valuable introduction to a book of this kind.

Next to its completeness, the most marked characteristic of the book is its lack of dogmatism. Correlated with caution is a tendency to entertain the idea of multiple origin of apparently natural groups, and to admit question, even where affinity seems best established. Two examples: the probable central position of some such plant as *Anthoceros* in the ancestry of Embryophyta is perfectly presented, and the group "Anthocerotes" is made a class, coordinate with Hepaticæ and Musci. The latter are treated as probable derived groups, but the derivation seems to be pictured as exceedingly ancient, from primeval Anthocerotes, of which "Of course, the sporophyte . . . must have been much simpler than in any living forms—perhaps comparable to that of such liverworts as *Riccia* or *Sphaerocarpus*." To the reviewer, the stoma, common to *Anthoceros* and many mosses, provides positive proof that their common ancestor, if not exactly *Anthoceros* itself, had at any rate a sporophyte independent enough in its nutrition to have evolved this structure.



As to the angiosperms, polyphyletic is explicitly advocated. The characteristic structure of this group is not seed, nor flower, nor pollen tube, nor trachea; it is the embryo-sac. If the hypothesis of multiple origins means that this structure has been evolved several times independently, it is hard to accept. Even more than the stoma, it requires good evidence of repeated evolution before it is questioned as proof of real affinity.

There are 351 numbered figures, most of which are composed of a considerable number of drawings, largely original and well reproduced. They add materially to the value of the book. The text is a remarkable mine of detailed information. How much there is of this may be shown by the index, which occupies 37 pages of fine print, two columns to the page, and is still incomplete; thus, under "stoma" there is no reference to the text, and under "embryo-sac" there is only one.—E. B. COPELAND, Department of Botany, University of California, Berkeley.

*Sinopsis de la Flora del Cuzco.* FORTUNATO L. HERRERA. Tomo I. Parte Sistemática. Pag. 1-528. Publicado bajo los auspicios del supremo gobierno. Lima, Peru, 4 de Julio, 1941.

This check list of the plants of the Department of Cuzco by the distinguished Peruvian botanist is by far the most complete of several similar works by the same author, the first of which appeared in 1919. It lists 2166 species (with a few varieties) 588 of which are cryptogams, about 250 of these being ferns and fern allies. Even so, the author suggests that probably only about one-half of the species growing within the area have been recorded. The predominant families are Compositae, Gramineae, and Leguminosae.

The names are accompanied, at least for the phanerogams, by source of publication and citation of specimens. The latter are given in detail, usually including altitude, information which will be invaluable in any study of the flora; habitats, however, are rarely indicated. Often the range of the plant outside of Cuzco, if known, is mentioned; there are some economic notes. An appendix contains descriptions of new species based on the author's collections. There is also a list of native names and their scientific equivalents, and an index to the genera.

In a work of this nature, based of necessity on the literature available—of which there is a good bibliography—there are of course always omissions; on the other hand there are a few additions to the flora of Cuzco. In supplements, which it is to be hoped will be issued from time to time, it would be well to give the source of determination and to indicate where the collections may be consulted in order that identifications may be checked when desired. The work would be more consistently useful, too, if publication citations were always given (which is obviously the intent but they are not infrequently omitted). Most of the typographical errors will easily be corrected; only one mistake in the

presentation of the material has been noted, namely the including of the composite *Orthopappus*, on page 321, in the Melastomataceae.

The author in preparing the work and the Peruvian Government in publishing it have made a meritorious contribution to the scientific study of the rich and useful flora of Cuzco; may there be many more similar endeavors based increasingly on the activities of Peruvian students.—J. F. MACBRIDE, Field Museum of Natural History.

*A Flora of Arizona and New Mexico.* By IVAR TIDESTROM and SISTER TERESITA KITTELL. Pp. xxvi + 897 with frontispiece. The Catholic University of America Press, Washington, D. C., 1941. \$5.00.

The flora of Arizona and New Mexico, listing 898 genera and 3975 species, is arranged according to the systems of DeCandolle and Bentham and Hooker with some slight emendations, chief of which is the arrangement of the orders and families in a descending numerical sequence as to the number of cotyledons. Hence the Coniferae with many cotyledons come first and the ferns and fern allies with none appear at the close of the work. The keys are brief and to the point and brief descriptions aid materially in amplifying the keys. There is a general citation of habitat and range accompanying each entity. The work is ambitious and as such is worthy but one cannot read it without a feeling of regret. Much of the advance in botany of the past fifteen years is ignored. Many monographs which have appeared during this time are not alluded to either as to the species accepted or in the synonymy.

The frontispiece is a map of Arizona and New Mexico showing the major rivers and the two thousand foot contour intervals. There are fifteen circles indicating localities but no evident reference to these in the text. On the other hand the table of contents refers to the map as showing the "belts of vegetation." The reason for this confusion is not clear to the reviewer.

The volume is lithoprinted and would have been materially improved by either a little more space between the species or by underlining the species names. As it stands the pages appear crowded and the typography does not invite the reader's attention. In many instances the craftsmanship of both typist and printer is definitely at fault.—HERBERT L. MASON.

#### NOTES AND NEWS

On May 24, 1941, the University of California conferred the honorary degree of doctor of laws on Dr. Willis Linn Jepson, Professor of Botany Emeritus of that institution. The honor is in recognition of Dr. Jepson's contribution to our knowledge of the California flora and his long and successful promotion of forest conservation in the state.